Thorp and Covich's Freshwater Invertebrates • Fourth Edition

Volume IV: **Keys to Palaearctic Fauna**

Edited by D. Christopher Rogers and James H. Thorp

This multivolume series covering inland water invertebrates of the world began with Vol. I: Ecology and General Biology (2015) and was followed with identification keys for general invertebrates of the Nearctic in Vol. II (2016) and Neotropical Hexapoda (insects and springtails) in Vol. III (2018). It now continues with identification keys for Palaearctic invertebrates in Vol. IV. Three other volumes currently in development focus on general invertebrates of the Neotropical/Antarctic, Australasian, and Afrotropical Bioregions. In the initial planning stages are two volumes covering tropical Asia and Oceana, one on general invertebrates and the other on Hexapoda. All volumes are designed for multiple uses and levels of expertise by professionals in universities, government agencies, and private companies, as well as by graduate and undergraduate students.

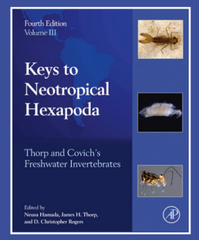
Key Features of Volume IV

- This volume provides identification keys for inland water (fresh to saline) invertebrates of the Palaearctic Zoogeographic Region from Iceland to Russia and from the northern pole region to Saharan Africa in the west, through the Middle East, to central China and Japan in the east.
- Identification keys for aquatic invertebrates to genus or species level for many groups and to family for Hexapoda, with the keys progressing from higher to lower taxonomic levels appropriate for the users' level of scientific knowledge and needs.
- A general introduction and sections on limitations, terminology and morphology, material preparation and preservation, and references for each group.



Also in This Book Series:
James H. Thorp & D. Christopher Rogers (editors). 2015. Ecology and General Biology. Volume I. Academic Press, Boston. 1118 p. ISBN: 978-0-12-385026-3.

Volume I describes the general ecology and biology of inland water invertebrates of the world. It is meant as a companion book for all taxonomic focused volumes (10 or 11) planned for the fourth edition, each of which will provide taxonomic keys for various zoogeographic regions. This volume includes an introductory chapter and five chapters on habitat characteristics, collection and culturing techniques, ecological relationships, invasive alien species, and economic impacts. These six chapters are followed by 35 chapters on the ecology and general biology of various taxonomic groups from protozoa to insect orders. Extensive literature references are provided in each chapter.



Also from Academic Press, Elsevier:
Neusa Hamada, James H. Thorp & D. Christopher Rogers (editors). 2018. Keys to Neotropical Hexapoda. Volume III, Academic Press, Boston. 811 p. ISBN: 9780128042236.

Volume III contains zoogeographic coverage of the entire Neotropical Region from central México and the Caribbean Islands poleward to the tip of South America. In addition to an introductory chapter and one on Collembola (springtails), another 41 chapters are focused at the ordinal, superfamily, or family levels, with keys to lower taxonomic levels for various aquatic insect groups, depending on the current knowledge base.

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D. Christopher Rogers
James H. Thorp
Editors

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D. Christopher Rogers and James H. Thorp







Keys to Palaearctic Fauna

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James H. Thorp and D. Christopher Rogers
First Edition (2011)

Keys to Palaearctic Fauna

Thorp and Covich's Freshwater Invertebrates — Volume IV

Fourth Edition

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Dedications From the Editors

To our authors who made this book possible.

D. Christopher Rogers

To my loving wife of nearly half a century who has tolerated my occasional frustrations with my profession while showing great interest in my studies, and to the students working in my lab over the decades who have never failed to inspire and challenge me while reinforcing in my mind the true value of being a professor.

James H. Thorp

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About the Editors



Dr. D. Christopher Rogers is a research zoologist at the University of Kansas with the Kansas Biological Survey and is affiliated with the Biodiversity Institute. He received his Ph.D. degree from the University of New England in Armidale, NSW, Australia. Christopher specializes in freshwater crustaceans (particularly Branchiopoda and Malacostraca) and the invertebrate fauna of seasonally astatic wetlands on a global scale. He has numerous peer-reviewed publications in crustacean taxonomy and invertebrate ecology, as well as published popular and scientific field guides and identification manuals to freshwater invertebrates. Christopher is an Associate Editor for the Journal of Crustacean Biology and a founding member of the Southwest Association of Freshwater Invertebrate Taxonomists. He has been involved in aquatic invertebrate conservation efforts all over the world.



Dr. James H. Thorp has been a Professor in the Department of Ecology and Evolutionary Biology at the University of Kansas (Lawrence, KS, USA) and a Senior Scientist in the Kansas Biological Survey since 2001. Prior to returning to his alma mater, Prof. Thorp was a Distinguished Professor and Dean at Clarkson University, Department Chair and Professor at the University of Louisville, Associate Professor and Director of the Calder Ecology Center of Fordham University, Visiting Associate Professor at Cornell, and Research Ecologist at the University of Georgia's Savannah River Ecology Laboratory. He received his Baccalaureate from the University of Kansas (KU) and both Masters and Ph.D. degrees from North Carolina State. Those degrees focused on zoology, ecology, and marine biology, with an emphasis on the ecology of freshwater and marine invertebrates. Dr. Thorp has been on the editorial board of three freshwater journals and is a former President of the International Society for River Science. He teaches freshwater, marine, and invertebrate courses at KU, and his Masters and Doctoral graduate students work on various aspects of the ecology of communities through macrosystems in rivers, reservoirs, and wetlands. Prof. Thorp's research interests and background are highly diverse and span the gamut from organismal biology to community, ecosystem, and macrosystem ecology. He works on both fundamental and applied research topics using descriptive, experimental, and modeling approaches in the field and lab. While his research emphasizes aquatic invertebrates, he also studies fish ecology, especially as related to food webs. He has published more than one hundred refereed journal articles, books, and chapters, including three single-volume editions of *Ecology and Classification of North American Freshwater Invertebrates* (edited by J.H. Thorp and A.P. Covich) and three volumes in the current fourth edition of *Thorp and Covich's Freshwater Invertebrates*.

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Preface to the Fourth Edition

Those readers familiar with the first three editions of our invertebrate book (*Ecology and Classification of North American Freshwater Invertebrates*, edited by J.H. Thorp and A.P. Covich) will note that the fourth edition has expanded from a North American focus to worldwide coverage of inland water invertebrates. We gave our book series on inland water invertebrates the name *Thorp and Covich's Freshwater Invertebrates* to: (1) associate present with past editions, unite current volumes, and link to future editions; (2) establish a connection between the ecological and general biology coverage in Volume I with the taxonomic keys in the remaining volumes; and (3) give credit to Professor Alan Covich for his work on the first three editions. For the sake of brevity, we refer to the current edition as T&C IV. Whether a fifth edition of T&C will ever appear is certainly problematic, but who knows? At present we are considering producing up to 12 volumes in the fourth edition.

While I am the sole editor of the "series" at this point, Dr. D. Christopher Rogers has been a major and highly valued partner in developing ideas for the fourth edition and is thus far a coeditor on the first four volumes in print (senior editor on the fourth) as well as on the three volumes in development. He is also likely to play a major role in many of the remaining volumes because of his diverse and global knowledge of freshwater invertebrates, especially in the area of taxonomy. As we made significant progress on the first seven volumes, we began contacting potential coeditors to develop two more volumes for another zoogeographic region, and negotiations with those potential editors are now underway. However, we are still seeking experts in fields of invertebrate taxonomy for various zoogeographic regions to serve as highly dependable coeditors, especially those who both work and live in the zoogeographic regions covered by the various future volumes.

Our concept for T&C IV included producing one book (Vol. I in 2015) with six chapters on general environmental issues applicable to many invertebrates, followed by 35 chapters devoted to individual taxa at various levels (order to phylum, or even multiple phyla in the case of the protozoa). Volume I was designed both as an independent book on ecology and general biology of the various freshwater invertebrate taxa and as a companion volume for users of the keys in the regional taxonomic volumes, thereby reducing the amount of information duplicated in the taxonomic volumes. The perhaps 11 taxonomic volumes we foresee publishing in this series will contain both keys for identifying invertebrates in specific zoogeographic regions and descriptions of detailed anatomical features needed to employ those keys.

While the vast majority of authors in T&C I–III were from the USA or Canada, we attempted in the global volumes of T&C IV to attract authors from many additional countries on six continents. Although we largely succeeded in this goal, we expect the fifth edition of T&C—if it is ever published—to continue increasing the proportion of authors from outside North America as our books become better known internationally.

Our goals for T&C IV are to improve the state of taxonomic and ecological knowledge of inland water invertebrates, to help protect our aquatic biodiversity, and to encourage more students to devote their careers to working with these fascinating organisms. These goals are especially important because the verified and probable losses of species in wetlands, ponds, lakes, creeks, and rivers around the globe exceed those in most terrestrial habitats.

James H. Thorp

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Preface to Volume IV

This is the fourth volume of the fourth edition of *Thorp and Covich's Freshwater Invertebrates* (T&C IV), and the second to focus on a bioregion outside the Nearctic. Information on the ecology and general biology of the groups can be found in Volume I (Ecology and General Biology, edited by Thorp & Rogers, 2015), the companion text for the current and all remaining books in this series. All taxonomic volumes (other than those focused exclusively on Hexapoda) are expected to consist of an introductory chapter, a chapter on protozoa (multiple kingdoms), and multiple chapters on individual phyla from Cnidaria to various groups within Arthropoda. Some of the chapters are very small (e.g., Chapter 14 on Entoprocta), whereas others are quite large. A major change in Volume IV is the division of the single chapter on Arthropoda found in Volume II (which represented more than half the pages of that volume) into a separate section encompassing six chapters.

A typical chapter includes a short introduction, a brief discussion of limits to identification of taxa in that chapter, important information on terminology and morphology that is needed to use the keys, techniques for preparing and preserving material for identification (also covered in Volume I), the taxonomic keys, and a few references. In the large chapters on Mollusca (11), Annelida (12), and Arthropoda (16–22), different individuals have contributed separate sections, and thus there are multiple sections on introduction through keys and references. While this may confuse some readers, it has allowed us to gain contributions from an increased number of experts around the world.

The multilevel keys are formatted to enable users to work easily at the level of their taxonomic expertise and the needs of their project. For that reason, we separated keys by major taxonomic divisions. For example, a student in a college course might work through one or more of the initial crustacean keys to determine the family in which a freshwater shrimp belongs. In contrast, someone working on an environmental monitoring project might need to identify a crayfish or crab to genus or even species, and thus would use the relevant, detailed keys that require more background experience. We also designed most keys, where possible, to proceed from a general to a specific character within a couplet.

We have asked authors to include only taxa that are recognized internationally by publication in reputable scientific journals which follow the International Code of Zoological Nomenclature. Thus, no taxa that have merely been proposed should have been included, even if they have been identified by the world's expert on that group. "Common" species are not designated in the keys themselves because a common species in one area may not be common in another, and this designation can lead to overly frequent and false identifications. Authors have been encouraged to end the keys at the point where further identification without genetic analysis is not practical or when it is clear that too many of the extant fauna have yet to be described in scientific publications.

Users of these keys need to realize that taxonomy is a growing and vibrant field in which new taxa are being described and previously accepted relationships re-evaluated. For some users, this volume may be sufficient for their needs, but for others a companion text listing known species in a smaller geographic region may also be helpful.

This edition is strongly focused on species found in fresh through saline inland waters, with a nonexclusive emphasis on surface waters, thereby reflecting the bias of existing scientific literature. Again, most estuarine and parasitic species are not covered in this book, but we do discuss species whose life cycle includes a free-living stage (e.g., Nematomorpha) and species that live in hard freshwaters through to brackish waters, even though they may be normally associated with estuarine or marine habitats in some parts of their life cycles (e.g., some shrimp and crabs).

It is our hope that scientists and students from around the world will benefit from this volume, especially those studying organisms in the Palaearctic. Suggestions for improving future volumes are welcomed.

Editors
D. Christopher Rogers
James H. Thorp

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Acknowledgments for Volume IV

Many people contributed to this volume in addition to the chapter authors and those acknowledged in individual chapters. We greatly appreciate all our colleagues who have contributed information, figures, or reviews to Volume III and also thank those who provided similar services for the earlier editions, upon which the present book partially relies. We are again grateful to the highly competent people at Academic Press/Elsevier who helped in many aspects of the book's production from the original concept to the final marketing. In particular, we appreciate our association with Elsevier editors including Emily Thomson and Louisa Munro and earlier Laura Kelleher, as well as the entire global production teams for Elsevier.

D. Christopher Rogers
James H. Thorp

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Chapter 1

Introduction[1]

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Chapter Outline

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INTRODUCTION TO THIS SERIES, VOLUME, AND CHAPTER

The first volume of *Thorp and Covich's Freshwater Invertebrates* (Thorp & Rogers, 2015) provided global coverage of the ecology, general biology, phylogeny, and collection techniques for inland water invertebrates. The focus of all volumes in our series after Volume I has been or will be on taxonomic keys for individual bioregions of the world. The taxonomic keys provide users with means to work at their level of need and expertise. Our authors have tried to limit the specificity of the keys to those taxa where comprehensive knowledge is available for most taxa in a particular group or where identification is only possible for certain life stages. It is our hope that these books demonstrate the limits of our knowledge on the biodiversity for different regions and taxa, and thus will inspire future studies in those areas.

In addition to the first four volumes currently in print (Thorp & Rogers, 2015, 2016; Hamada et al., 2019; and the current volume), two volumes in the series may appear in 2019–2020: (1) Keys to Neotropical and Antarctic Fauna (Damborenea et al., 2019, in prep.); and (2) Keys to Australasian Fauna (Ahyong et al., 2020, in prep). Future volumes will cover Afrotropical Fauna (Day et al.; perhaps in 2022) and Oriental/Oceana fauna (each with one to two volumes) as well as more detailed coverage of Hexapoda in the Nearctic and Palaearctic Bioregions. We consider this series of 10–12 volumes to be a globally expanded, fourth edition of the earlier *Ecology and Classification of North American Freshwater Invertebrates* (edited by Thorp & Covich in 1991, 2001, and 2010). While some labs may have multiple copies of the "Keys to Fauna" in their region, we also recommend that they have at least one copy of Volume I to obtain useful background information on each invertebrate group.

The current chapter is organized into an introduction, a description of the taxonomic focus of this particular volume, a section explaining the organization of most taxonomic chapters, and a key to larger taxonomic groups. This chapter's key is designed to help the reader locate the most pertinent chapter (a task probably useful mostly for students and relatively novice taxonomists) and begin identifying organisms in their samples. Readers will note that chapters within and among volumes vary in the specificity of their taxonomic keys. This reflects both the likely percent of the fauna that has been named and how easily taxa can be separated by alpha taxonomic methods and associated keys. While there are occasional references to genetic separation of taxa, the keys are primarily based on microscope identifications.

1 This chapter was written to be a useful starting point for the previous, current, and future taxonomic volumes in all zoogeographic regions. Consequently, there will be only minor to moderate differences in this chapter among various volumes.

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NATURE AND FAUNA OF THE PALAEARCTIC BIOREGION

As is clear from the title, this volume covers inland aquatic invertebrates of the Palaearctic, a bioregion that stretches from Iceland in the west to Japan in the east. It also includes inland waters along the Arctic Sea south to northern Africa, the Middle East, and northern China. Taxa in this area occur from low to high altitude sites of varying temperatures, as well as from areas influenced by coastal and inland climatic zones. Unlike our previous books, this volume has extensive coverage of a deep, ancient lake (Lake Baikal) and major inland water saline systems (the Ponto-Caspian region, the Azov Sea, and the Dead Sea). Moreover, the great ecological variation of this bioregion includes hot and cold deserts, temperate steppes, tundra, and forested regions, with concomitant variation in their invertebrate fauna. Many of these diverse habitats are described in Chapter 2 of Volume I. Chapters 2–22 include a comprehensive coverage of the fauna of the Palaearctic, but many poorly studied areas and taxa exist, particularly in central Asia, western China, and Mongolia. The Palaearctic fauna described in this volume overlaps to a minor extent with those in the Nearctic, Afrotropical, and Oriental bioregions and thus with our volumes covering those fauna.

Not all taxa are equally covered in this volume. In some cases, this is intentional, as in limiting Hexapoda to family level (anticipating a large, future volume on insects of this bioregion). In a few other cases (notably with Arachnida), extensive attempts to find qualified authors proved fruitless except for one group. Finally, the taxonomic knowledge of some groups (e.g., Amphipoda) is vastly more extensive than for other taxa as a result of the abundance of invertebrate species and the number of scientists dedicated to studying them.

COMPONENTS OF TAXONOMIC CHAPTERS

This volume is an identification manual to the inland water invertebrates of the Palaearctic in which we present information needed to diagnose and assign these organisms to various taxonomic levels. Other information concerning ecology, morphology, physiology, phylogeny, and both collecting and culturing techniques can be found in Volume I of this series. Most of the chapters in the current volume are limited to a single phylum. Exceptions are Chapter 2 (multiple kingdoms of protozoa) and the seven chapters on Arthropoda. We have attempted to include the following six sections in each of those chapters: (1) a brief overview of the higher level taxon; (2) a description of identification limitations for each taxon; (3) details of pertinent terminology and morphology; (4) information on preparing and preserving specimens for identification; (5) taxonomic keys (separated by level of identification); and (6) a shortened list of references. Readers can find a much more extensive list of references to their group in Volume I (Chapters 3 and 7–41) along with more details on collecting, preparation, and preserving major taxa. Figures in each chapter are limited to those needed for effective use of the keys. For additional anatomical information, including figures, see the relevant chapter in Volume I.

HOW TO USE THIS VOLUME

There is an old maxim that says, "keys are written by people who do not need them for people who cannot use them." Nonetheless, we have made every effort to make these keys as user friendly as publication limitations would permit.

Each chapter includes a basic introduction to the morphology and terminology used in diagnosing the taxa of that section. Limitations to the current state of taxonomic knowledge are also presented so that the reader may gauge the reliability of the information presented. Only the established, peer-reviewed scientific literature is used to define the taxonomic categories and epithets included. All names, as far as we are aware, conform to the International Code of Zoological Nomenclature. All nomina and taxonomic arrangements used, as well as the rejection of old names are based on peer-reviewed scientific literature. Names from unpublished manuscripts, dissertations, "in-house" designations, or records that have not been validated are not included. Provisional names and species designated "taxon 1" or "species 1" are not used unless they were previously recognized and accepted in the peer-reviewed scientific literature (Richards & Rogers, 2011). No new species descriptions or previously unpublished taxonomic arrangements are presented.

The keys are dichotomous (no triplets or quadruplets are used) and are hierarchical. Thus, for a given group, the first keys are to the highest taxonomic category. The second set of keys is to the next level, the third set to the level below that one, and so on, down to the lowest justifiable taxonomic level based on current knowledge of that group. This level is different for different groups depending upon the state of resolution in the scientific literature. Organisms not identifiable beyond a particular taxonomic level are left at that level.

Properly prepared keys typically employ specific, primary, diagnostic characters. Older keys often use different characters than the more recent keys. This shift in primary characters results from systematists and taxonomists testing the importance of characters. The ultimate goal of the systematist is to have the taxonomic characters used in our keys converge as closely as possible with biological reality. To a nontaxonomist, the resulting process may erroneously seem merely to be "lumping and splitting" taxonomic

groups rather than the result of employing the scientific method to reveal natural relationships.

Surprisingly, many users do not know how to interpret a dichotomous key, making the fundamental assumption that a correct identification answer is always present in the key. This assumption generally takes one of the following three forms:

1. *All species are identifiable using a given key.* Many new species have yet to be discovered, let alone described. Generalized geographic ranges are provided for most taxa presented herein, yet species ranges shrink, swell, and change elevation constantly, particularly as weather and climate patterns shift. Species disperse, colonize, and suffer stochastic local extinctions. In addition to these natural processes, some species are introduced intentionally or accidentally by humans, and sometimes their establishment allows other species to invade as well. Furthermore, some regions are better studied than others; many parts of the world have not been explored, nor the fauna described. There are still plenty of new taxa to encounter.
2. *All variation is accounted for in the key.* As stated earlier, identification keys use specific, primary, diagnostic characters. Problems in identification are compounded by taxa that: (1) have different character states at different times; (2) only have diagnostic characters at certain life stages or in certain genders; and/or (3) have severely truncated morphology (often due to lack of sexual selection) and lack morphological characters to separate the species. Furthermore, new variation within taxa is continually developing, and thus one cannot assume that species are immutable or develop tools predicting those changes.
3. *The key is a sufficient identification tool in and of itself.* A key is just a tool. The fact that one has a bolt that needs removing and a wrench of the correct size does not mean that the bolt can be loosened. Similarly, identification keys are tools to aid in taxon identification. They are primarily tools to eliminate incorrect taxa from the range of possible choices, narrowing the field to the names that may be applicable. Keys are the process of elimination. The possibility that the specimen to be identified is new, a hybrid, anomalous, or a recent invasive colonist is always a possible answer. This is fundamental to using any identification key.

Once one arrives at a name or group of possible names for a specimen in hand, the specimen should then be compared against descriptions, distribution maps, and figures of that and other taxa in that group. The descriptions, figures, and maps are other tools to be used in identification. Direct comparison of the specimen at hand with identified museum material or using molecular comparisons is also sometimes necessary for correct identification.

Species are not immutable, fixed in location and form. They change constantly and will continue to do so, confounding keys and any other identification method, such as trait tables, character matrices, or even genetic analyses. This is why biology is far behind physics in the development of unified theories; biology is far more complex than physics, as it involves more mutable interacting parts and processes.

KEYS TO MAJOR TAXA OF INLAND WATER INVERTEBRATES OF THE PALAEARCTIC

A major change in the identification keys for our fourth edition has been to include multiple keys per chapter that generally start with a class-level key and proceed to finer and finer divisions. These allow users to work at their levels of interest, need, and skill without having to wade through extraneous taxa not in the direct line to the taxon of interest.

The following key was derived in part from Chapter 1 in Volume I of the fourth edition. It is meant to allow you to move to the next level of keys, which will be in individual chapters.

1	Multicellular, heterotrophic organisms as individuals or colonies (sometimes with symbiotic autotrophs) ..... kingdom Animalia 2
1′	Unicellular (or acellular) organisms present as individuals or colonies with nuclei irregularly arranged; heterotrophic and/or autotrophic; multiple phyla within the autotrophic protozoa phyla ..... kingdom Protista [Chapter 2]
2(1)	Radially symmetric or radially asymmetric organisms living individually or in colonies 3
2′	Individuals bilaterally symmetric 4
3(2)	Surface not porus; oral tentacles always present around a closeable mouth; colonial or single, mostly single polyp forms (primarily hydra) or rarely medusoid form (freshwater jellyfish; adults with a single central body cavity opening to the exterior and surrounded by cellular endoderm, acellular mesoglea, and cellular ectoderm ..... phylum Cnidaria [Chapter 4]
3′	Surface porus; colonial; tentacles absent; no closable orifices; without discrete organs; cellular-level (or incipient tissue-level) construction; variable, nondistinct colony shapes, including encrusting, rounded, or digitiform growth forms; skeleton of individual siliceous spicules and a collagen matrix; internal water canal system; may contain symbiotic algae; the sponges ..... phylum Porifera [Chapter 3]
4(2)	Oral region with numerous tentacles or cilia distributed around the mouth; organism never with eversible jaws and never vermiform as adult 5

4	Oral region with two or no tentacles, or tentacles behind the mouth	7
5(4)	Oral region with tentacles, organisms in gelatinoids or branching colonies	6
5′	Oral region ringed with cilia, muscular pharynx (mastax) with complex set of jaws; single free swimming, or semi-sessile living singly or in small colonies; wheel animals, or rotifers	phylum Rotifera [Chapter 8]
6(5)	Oral tentacles (the lophophore) in a "U" or "horseshoe" shape around mouth; anus opens outside of lophophore; colonial animals, often in massive colonies attached to hard surfaces; true bryozoans	phylum Ectoprocta (Bryozoa) (Chapter 13)
6′	Both mouth and anus open within lophophore; individual (noncolonial) animals with a calyx containing a single whorl of 8−16 ciliated tentacles	phylum Entoprocta [Chapter 14]
7(4)	Not with the combination of characteristics described below	8
7′	Small (50−800 μm), spindle- or tenpin-shaped, ventrally flattened with a more or less distinct head bearing sensory cilia; cuticle usually ornamented with spines or scales of various shapes; posterior of body often formed into a furca with distal adhesive tubes; gastrotrichs (pseudocoelomates)	phylum Gastrotricha [Chapter 7]
8(7)	Anterior mouth and posterior anus present	9
8′	Flattened or cylindrical, acoelomate worms with only one ventral digestive tract opening; sometimes with evident head; turbellarian flatworms (commonly called planaria, a nonspecific, and usually incorrect name)	phylum Platyhelminthes [Chapter 5]
9(8)	Vermiform or not, eversible oral proboscis not present, although eversible jaws or other mouthparts may occur	10
9′	Long, flattened, unsegmented worms with an eversible proboscis; ribbon worms	phylum Nemertea [Chapter 6]
10(9)	Body not enclosed in a single, spiraled shell or in a hinged, bivalved shell; or if a bivalved shell is present, then animal has jointed legs	11
10′	Soft-bodied coelomates whose viscera is covered (in freshwater species) by a single or dual (hinged), hard calcareous shell; with a ventral muscular foot; fleshy mantle covers internal organs; snails, clams, and mussels	phylum Mollusca [Chapter 11]
11(10)	Segmented legs absent in all life stages; if jaws are present, then body with at least 20 segments	12
11′	Adults and most larval stages with legs; if larvae are without legs or prolegs (some insects), then cephalic region with paired mandibles, or eversible head, always with less than 15 body segments	14
12(11)	Organism vermiform, not segmented	13
12′	Organism vermiform or not, body segmented	phylum Annelida [Chapter 12]
13(12)	Body cylindrical, usually tapering at both ends; cuticle without cilia, often with striations, punctuations, minute bristles, etc.; 1 cm long (except family Mermithidae, <6 cm); nematodes, roundworms	phylum Nemata [Chapter 9]
13′	Body with anterior tip normally obtusely rounded or blunt, posterior tip may be bi- or trilobed; cuticle opaque to dark brown or black, and epicuticle usually crisscrossed by minute grooves; length several cm to 1 m, width 0.25−3 mm; only adults with free-living stage; hairworms or horsehair worms	phylum Nematomorpha [Chapter 10]
14(11)	Four pairs of clawed, nonjointed legs; water bears	phylum Tardigrada [Chapter 15]
14′	Adults and most larvae with jointed legs, or legs lacking, or more or less than four pairs	phylum Arthropoda [Chapter 16][2]

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2 Chapter 16 includes a key that will lead to subsequent chapters covering this phylum.

Part I

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Chapter 2

Protozoa

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PROTOZOA

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INTRODUCTION

During the last 20 years, studies on the systematics and evolution of unicellular eukaryotes (algae, protozoa, and lower fungi) have been in a state of great activity. Over this period, many taxonomic boundaries, including those between the algae and protozoa, have been broken down and new relationships established (Cavalier-Smith, 2010; Adl et al., 2012; Ruggerio et al., 2015). As a result, the constituent organisms are grouped together by some workers as protists, reviving the term originally coined by Haekel (1866), or as protoctists (Margulis et al., 1989), although many systematists believe that such groups have no evolutionary or systematic validity. By contrast, other workers have proposed systems that retain the kingdom Protozoa, albeit with much modified definitions and boundaries (Cavalier-Smith, 2010; Ruggerio et al., 2015). Nevertheless, the terms algae and protozoa are still useful in a functional or ecological sense defining (primarily) photoautotrophic and heterotrophic protists, respectively.

Protozoa *sensu lato*, which means first animals, are a diverse assemblage that comprises a number of separate lineages representing almost all the major eukaryote clades, including alveolates, stramenopiles, amoebozoans, opisthokonts, rhizarians, and excavates (Cavalier-Smith, 2010; Adl et al., 2012; Ruggerio et al., 2015). Protozoa typically measure 5−1000 μm in size, and most are visible only with the aid of a microscope. There is considerable morphological and physiological diversity within the group. Because actively feeding protozoa need water, all free-living (nonparasitic) protozoa are essentially aquatic, living in freshwater (including soil), brackish, and marine environments.

LIMITATIONS

There are a number of factors that pose significant limitations to the taxonomy of protozoa. These include: (1) the lack of adequate methods for the fixation and long-term preservation of specimens for much of the ca. 350-year history of the discipline of protozoology; (2) an absence of type specimens for most species; (3) a lack of sufficient morphological features for species circumscription; (4) inadequate species descriptions for reliable identification; (5) high rates of synonymy; (6) insufficient numbers of trained taxonomists; (7) undersampling and a large unknown species diversity; and (8) technical difficulties in culturing many species, which is sometimes a prerequisite for adequate characterization.

It is often difficult and time-consuming to identify protozoa to the level of species. In many cases, unambiguous identification requires specialized staining techniques or the use of electron microscopy. The taxonomic grouping used in our key is an amalgamation of publications by specialists on the different groups (e.g., Lee et al., 2000; Lynn, 2008; Bass et al., 2009; Cavalier-Smith, 2010; Smirnov et al., 2011; Adl et al., 2012; Ruggerio et al., 2015). While the taxonomy of many groups is based on a combination of cell morphology, ultrastructural features, and molecular data, this key is designed to make possible the identification of many protozoa to the family level using light microscopy alone. Although observation of living organisms is important for identification, the key should still be useful for many fixed samples. The illustrations used as examples here are of one or more species considered typical of a genus.

Although this key primarily deals with free-living protozoa, some ciliates that are commensal or parasitic (e.g., certain groups of suctorians and oligohymenophoreans) are also included.

TERMINOLOGY AND MORPHOLOGY

Traditionally, free-living protozoa have been divided into three main groups according to their morphology and means of locomotion: flagellates, amoebae (including heliozoans), and ciliates (Fig. 2.1). Of these, only the ciliates are a truly natural, monophyletic group. The flagellates and amoebae are polyphyletic and include groups that may

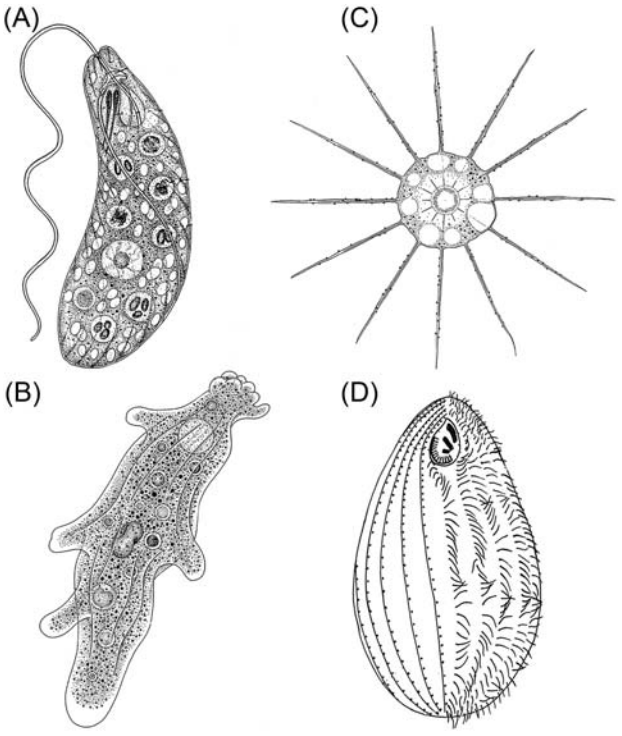


FIGURE 2.1 Examples of the main functional groups of protozoa. (A) *Peranema trichophorum* − a flagellate; (B) *Amoeba proteus* − an amoeba; (C) *Actinophrys sol* − a heliozoan; (D) *Tetrahymena* sp. − a ciliate. *After Vickerman & Cox (1967) (A and B); From Siemensma, Ferry J.; Page, F. C., Nackte rhizopoda und heliozoea, 1991. (C); Curds (1982).*

be only distantly related. Nevertheless, from a practical viewpoint, it is still sometimes useful to refer to these groupings because isolation, cultivation, and identification methods used are often the same within each group.

Flagellates

Flagellates are characterized by the possession of one or more flagella, which are long, tapering, hair-like appendages that act as organelles of locomotion and feeding (Figs. 2.1 A and 2.19 B). In free-living taxa, as opposed to parasitic species, the number of flagella is limited; *Paramastix* has two rows of 8−12 flagella, but most others have 1−4 (usually 2). Where two flagella are present, one typically projects forward and the other trails behind. Often, the organism's flagella are longer than its body. There are several groups of heterotrophic flagellates in fresh water: choanoflagellates, kinetoplastids, diplomonads, and bicoecids. These are raised to phyla by some authors, while bicoecids are occasionally put with chrysophytes. Some amoeboid forms such as cercomonads and the Schizopyrenida, or amoeboflagellates, also have flagella but are treated here with the amoebae.

Other groups of flagellates contain mostly or entirely autotrophic forms with chloroplasts. However, many of the pigmented, autotrophic taxa are also capable of phagotrophy, producing an overall condition called mixotrophy (Sanders, 1991; Esteban et al., 2010), and also among these groups are some wholly heterotrophic species. The groups with many mixotrophic or heterotrophic taxa include cryptophytes, chrysophytes, dinoflagellates, and euglenoids and are usually considered phyla. Pigmentation and chloroplast morphology are important taxonomic characters for some of these groups.

Choanoflagellates

These collared flagellates, are distinctive for the collar that surrounds the single flagellum (Figs. 2.2 B−H). They bear a strong resemblance to sponge choanocytes. Most choanoflagellates attach to the substrate or are colonial, and many have an external, loose-fitting covering or lorica, although this may be difficult to see with the light microscope.

Bicoecids

These protozoa (Fig. 2.2 I) resemble choanoflagellates, although they lack a collar. Like choanoflagellates, they are enclosed in a lorica and have a flagellum that is used to create a feeding current. A second flagellum lies along the cell and continues posteriorly to become an attachment to the base of the lorica.

Kinetoplastids

Kinetoplastids (Figs. 2.2 J, N−P) are known mostly as parasites, especially *Trypanosoma* and its relatives, but many members of the suborder Bodina live in fresh water (Vickerman, 1976). The best-known genus is *Bodo*, which, like other bodonids, has two flagella (Fig. 2.2 J), one of which trails, while the other extends ahead.

Cryptomonads

The cryptomonads include many common heterotrophs and autotrophs and a few mixotrophs. The two flagella are unequal in length and arise from a subapical invagination commonly referred to as a "gullet," although it does not appear to be the site of ingestion in heterotrophic forms. The pellicle is covered with plates, although these also are not generally visible.

Dinoflagellates

Dinoflagellates (Figs. 2.3 A−C and 2.19 C) form a very large and unique group that is probably more important in marine than freshwater environments. Their unique arrangement of flagella, one spiraling around the cell in a groove (girdle) and a second distally directed in another groove (sulcus), makes them distinctive. Again, heterotrophy and mixotrophy are common. A covering of plates may or may not be present (hence the terms armoured and naked dinoflagellates).

Chrysophytes

The generally small organisms prey on bacteria. They have two unequal flagella, one long and directed anteriorly, the other short and directed laterally (Figs. 2.3 K−M). They are naked or covered in fine siliceous scales (Esteban et al. 2012), which are not always visible with light microscopy; many are amoeboid. Their carbohydrate storage product, chrysolaminarin, occurs in liquid globules and may be useful in recognizing the members of this group. Chrysophytes contain both colorless heterotrophs and pigmented mixotrophs.

Euglenids

Euglenids are generally large flagellates with two flagella, although in many taxa only one flagellum emerges from the gullet (Fig. 2.3 D). Several heterotrophic species creep over the substrate with the second flagellum trailing and hidden beneath the cell (Figs. 2.3 F−H), as in some bodonids. The euglenids are currently assigned to the supergroup Excavata (Adl et al. 2012; Ruggerio et al., 2015).

Amoebae

The primary characteristic of amoebae is their possession of pseudopodia, retractile processes that serve as organelles

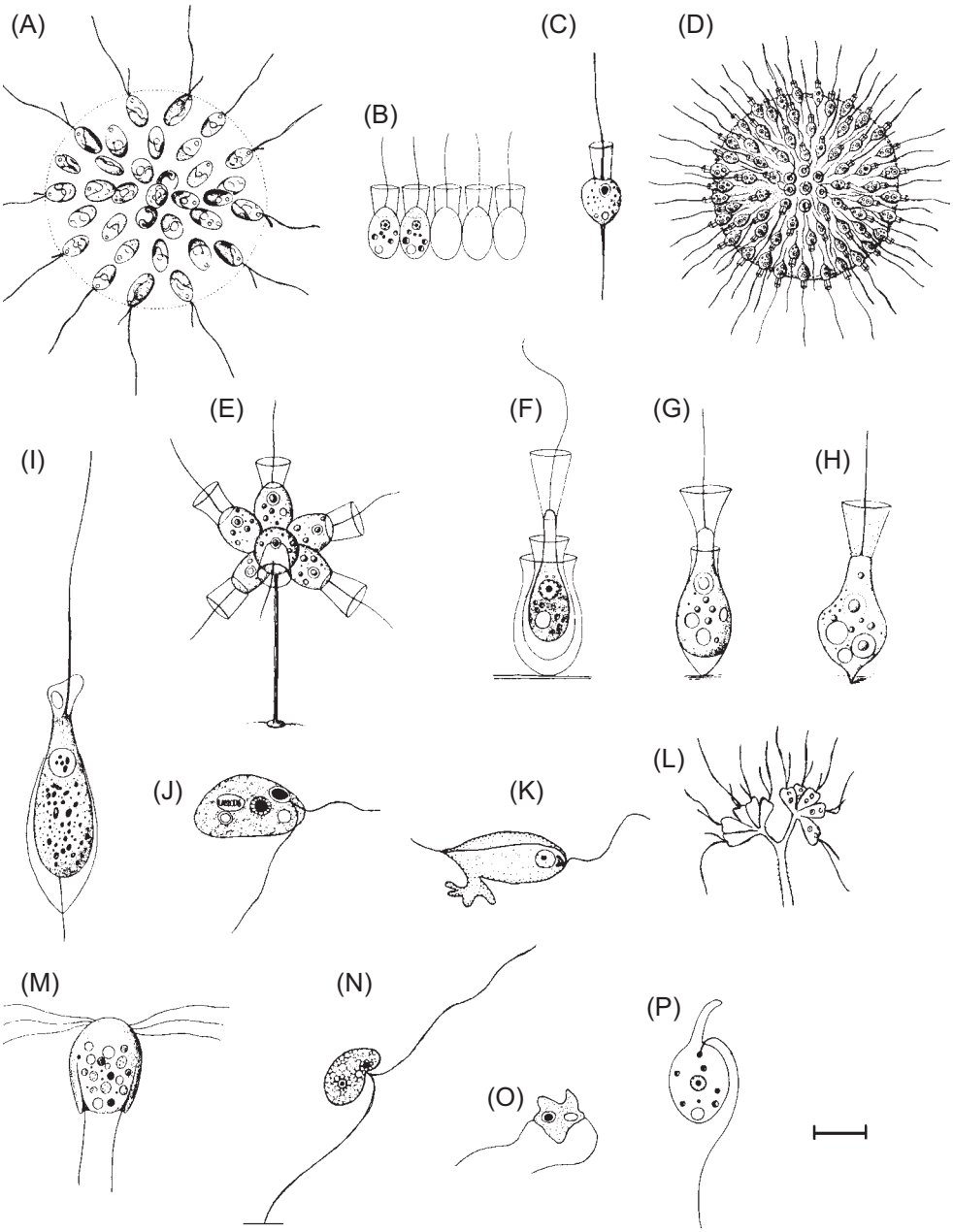


FIGURE 2.2 (A) *Uroglena americana* (mixotrophic); (B) *Desmarella moniliformis*; (C,D) *Sphaeroeca volvox*, individual and colony; (E) *Codosiga botrys*; (F) *Diploeca plactita*; (G) *Salpingoeca fusiformis*; (H) *Monosiga ovata*; (I) *Bioeca lacustris*; (J) *Bodo caudatus*; (K) *Cercomonas* sp.; (L) *Cephalomonas cyclopum*; (M) *Hexamita inflata*; (N and O) *Pleuromonas jaculans*, attached and amoeboflagellate forms; (P) *Rhynchomonas nasuta*. *After: Bourelly (1968) (L); Calaway and Lackey (1962); (N, O, and P) Lackey (1959); (B and F) Lee et al. (1985); (K); Pascher (1913) (C, D, E, G–J, and M). Scale 5 2.5 µm for P; 5 µm for (F, G–I, K, and L); 10 µm for (A–C, J, and M–O); and 20 µm for (E).*

of locomotion and feeding (Figs. 2.1 B and 2.19 A). There is considerable diversity of structure in the amoebae, particularly in the character of any shell or skeletal material that may be present, and in the type of pseudopodium, for example, broadly lobed, needle-like, or reticulate. Amoebae range in size from only a few micrometers to 2 mm in diameter. Although many lack a fixed external morphology, the characteristic morphologies shown by the various taxa are surprisingly distinctive even if difficult to quantify (Fig. 2.4). By using also the number, size, and structure of organelles and characteristics of tests (where present), identification is not as difficult for living specimens as might be imagined. The morphology of amoebae is plastic. Many adopt a stellate morphology if suspended in water, but few are truly planktonic, rather they live on surfaces or in sediments. In most *Amoeba* (Figs. 2.1 B and

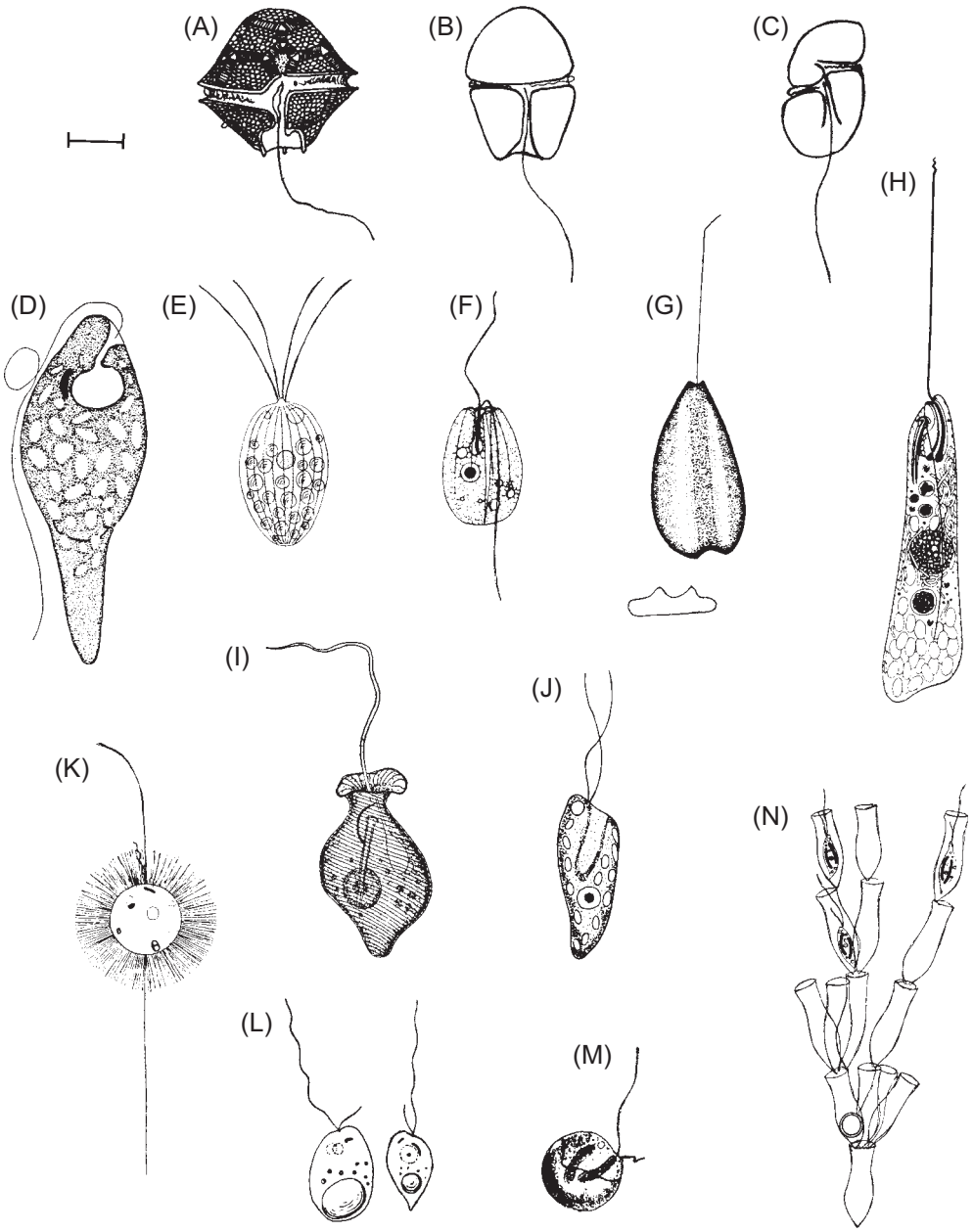


FIGURE 2.3 (A) *Peridinium*; (B) *Gymnodinium*; (C) *Gyrodinium*; (D) *Khawkinea halli*; (E) *Polytomella citri*; (F) *Entosiphon sulcatum*; (G) *Petalomonas abcissa*; (H) *Peranema trichophorum*; (I) *Spumella* (*Monas*) *vivpara*, two cell shapes; (J) *Chilomonas paramecium*; (K) *Paraphysomonas vestita*; (L) *Spumella* (*Monas*) *vivipara*, two cell shapes; (M) *Ochromonas variabilis*[a]; (N) *Dinobryon sertularia* (mixotrophic). *After: Bourelly (1968) (L); Calaway and Lackey (1962) (E, F, J, and N); Eddy (1930) (A); Jahn and McKibben (1937) (D); Leedale (1985) (H); Pascher (1913) (M); Lemmerman (1914) (K); Shawhan and Jahn (1947) (G); Smith (1950) (I). Scale 5 μm for (E); 10 μm for (A–C, G, and I–M); and 20 μm for (D, F, H, and N).*

2.4 F), for example, the cytoplasm is divided into an inner granular endoplasm and an outer hyaline ectoplasm, or hyaloplasm, with a characteristic thickness and distribution around the cell. Locomotion may be achieved by extending many pseudopodia simultaneously, as in *Amoeba* (Figs. 2.1 B and 2.4 F), or by moving as a single mass on a broad front (Figs. 2.4E, P), or as a cylinder (limax amoebae, Figs. 2.4 I, K, L). Not only do pseudopodia have characteristic shapes but the tail end or uroid may be distinctive (Figs. 2.4 J, L), and the cell surface may be distinctly sculptured, as in *Thecamoeba* (Fig. 2.4 D). The classification and systematics of the naked, lobose amoebae were recently revised by Smirnov et al. (2011) and Cavalier-Smith et al. (2015).

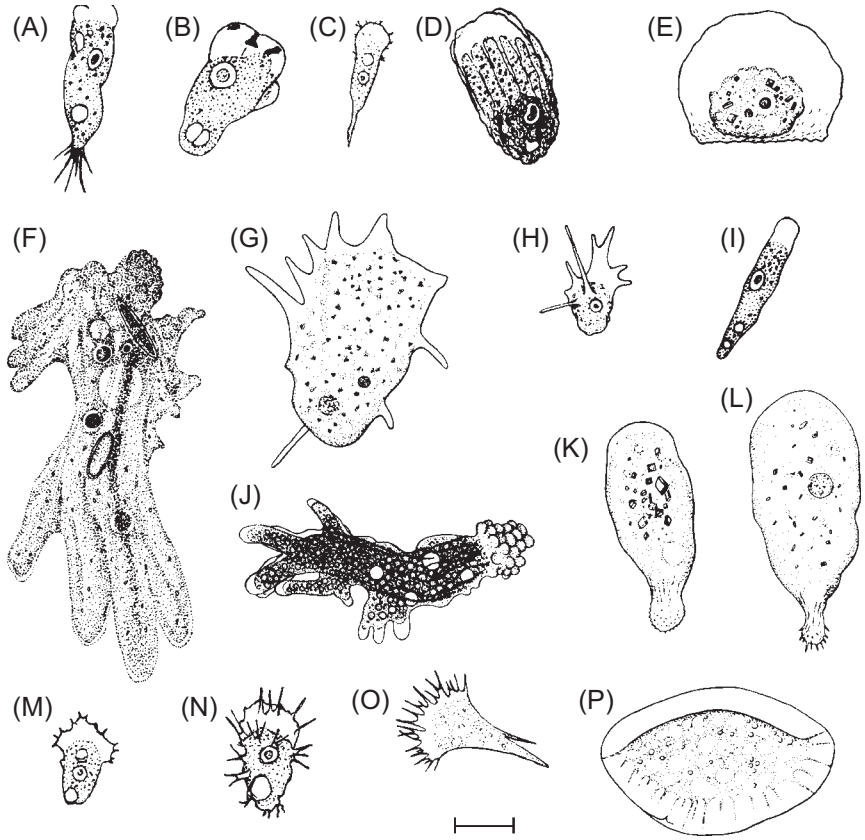


FIGURE 2.4 (A) *Vahlkampfia avaria*; (B) *Naegleria*; (C) *Stachyamoeba lipophora*; (D) *Thecamoeba sphaeronucleolus*; (E) *Vanella miroides*; (F) *Amoeba proteus*; (G) *Mayorella bigomma*; (H) *Vexillifera telemathalassa*; (I) *Hartmannella vermiformis*; (J) *Chaos illinoisense*; (K) *Saccamoeba lucens*; (L) *Trichamoeba cloaca*; (M) *Echinamoeba exudans;* (N) *Acanthamoeba*; (O) *Filamoeba nolandi*; (P) *Hylodiscus rubicundus*. *After: Bovee (1985) (A–D, H–J, and M–P); Kudo (1966) (F); Page (1988) (E, G, K, L, and P). Scale 5–10 µm for (A–C, E, I, and M); 15 µm for (H and N–P); 30 µm for (D, G, K, and L); 50 µm for (F); and 100 µm for (J).*

Other groups of amoebae, notably the testate amoebae, possess shells (or tests) that may be proteinaceous, agglutinate, siliceous, or calcareous in composition (Figs. 2.5 A–Q, 2.6 B–K and 2.9 H). These are generally vase-shaped, with a single opening through which pseudopodia emerge. Many are terrestrial, but benthic forms are common, and a few are planktonic. Identification of testate amoebae is mainly based on shell characters, i.e., size, shape, and composition.

Heliozoans

Heliozoans and pseudoheliozoans are roughly spherical amoebae with many stiff projections called axopodia radiating outward from the cell surface (Figs. 2.1 C, 2.7 and 2.8 D, E, I, J, L). The axopodia give heliozoans their characteristic sun-like appearance for which they are named, and are variously used for capturing food, sensation, movement, and attachment. Axopodia are strengthened by a microtubular array called an axoneme or stereoplasm. The term axoneme is also used to describe the microtubular core of cilia and flagella, but this does not imply homology and the origin and ultrastructure of axonemes is diverse (Yabuki et al., 2012). Most heliozoans lack the skeleton that is so characteristic of their marine counterparts such as Radiolaria and Acantharia, although some are covered in siliceous or organic scales (Figs. 2.7 F, H), and some have a perforated shell or capsule (order Desmothoracida, Fig. 2.7 A). Although heliozoans are frequently planktonic, they are found primarily on or near the benthos. Some heliozoans traverse the bottom with a unique tumbling motion resulting from controlled changes in the length of the axopodia. Many sessile forms with stalks are known. In sessile forms, cell division is likely to be unequal, producing a dispersal stage that may be flagellated or amoeboid. For a modern treatment of the taxonomy of heliozoans, see Cavalier-Smith and von der Heyden (2007).

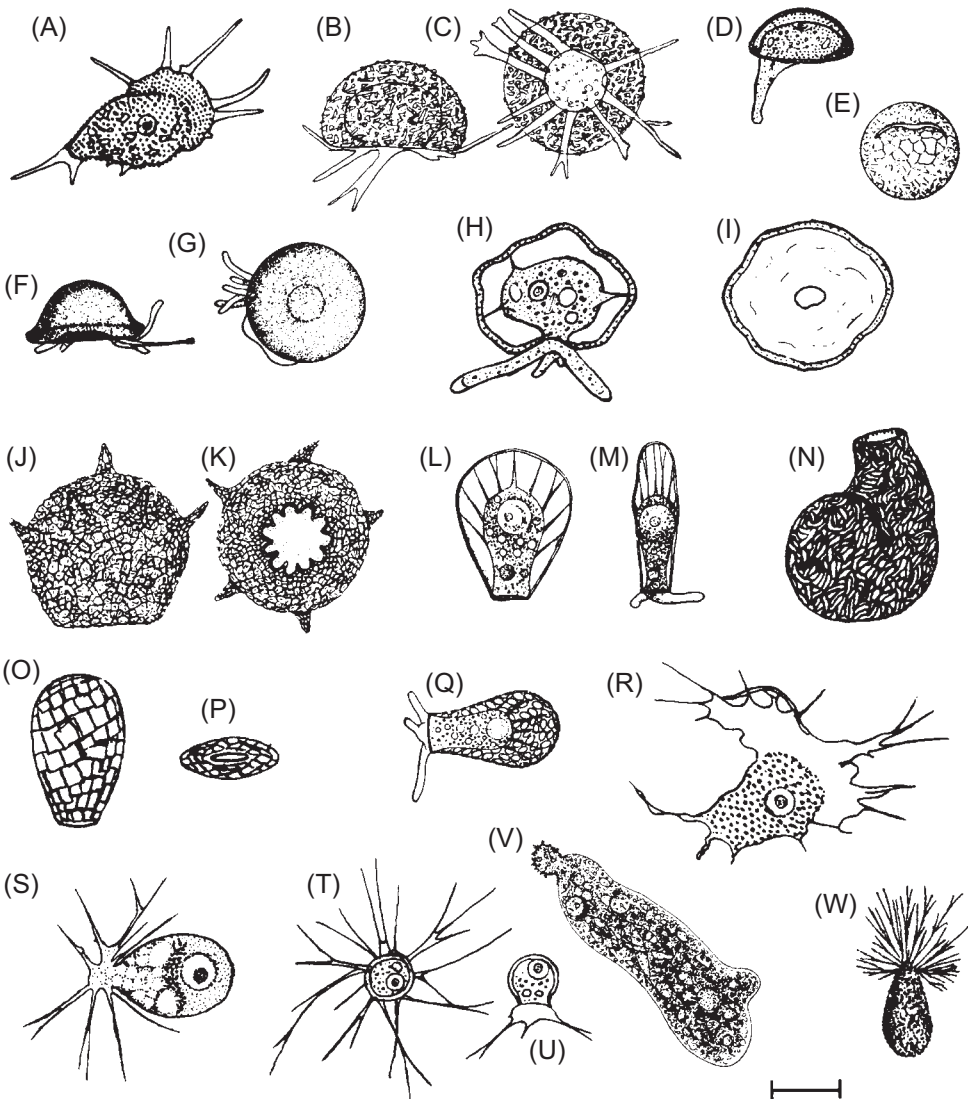


FIGURE 2.5 (A) *Cochliopodium bilimbosum*; (B and C) *Phryganella nidulus*, side and oral views; (D) *Pyxidicula operculata*; (E) *Plagiopyxis callida*; (F and G) *Arcella vulgaris*, side and dorsal views; (H and I) *Penardochlamys arcelloides*, side and oral views; (J and K) *Difflugia corona*, side and oral views; (L and M) *Hyalosphenia cuneata*; (N) *Lesquereusia spiralis*; (O and P) *Quadrulella symmetrica*; (Q) *Nebela collaris*; (R) *Penardia granulose*; (S) *Chlamydophrys minor*; (T and U) *Lecythium hyalinum*, dorsal and side views; (V) *Pelomyxa palustris*; (W) *Pseudo-difflugia gracilis*. *After: Bovee (1985) (A–C, H–K, N–P, R, T, and U); Deflandre (1959) (D–G, L, M, Q, S, and W); Kudo (1966) (V). Scale 5–10 μm for (C, R, and S); 30 μm for (L, T, and W); 45 μm for (N and O); 60 μm for (N and O); 90 μm for (B, E, F, and J); and 500 μm for (V).*

Ciliates

The ciliates (phylum Ciliophora) form a natural group distinguishable from other protozoa by a number of specialized features, including the possession of cilia, which are short hair-like processes, at some stage in their life cycle, the presence of two types of nuclei, and a unique form of sexual reproduction called conjugation. A representative ciliate is shown in Fig. 2.1 D. The body surface is covered with cilia, which are mostly aligned in rows called kineties. The pattern of kineties is interrupted in the region of the mouth where there may be specialized oral cilia used for feeding. The cilia may be reduced in number, especially in sessile forms, or organized into larger compound ciliary organelles such as cirri. The only large group that does not always possess cilia is the Suctoria; these are sessile predators whose dispersal stages are, however, ciliated. This distinctive group is easily recognized by its feeding tentacles. The novice should take care not to confuse small, ciliated animals with ciliates; the size range of ciliates overlaps that of several metazoan groups such as turbellarians, rotifers, and gastrotrichs. Some ciliates are mixotrophic due to the presence of endosymbiotic algae, or by

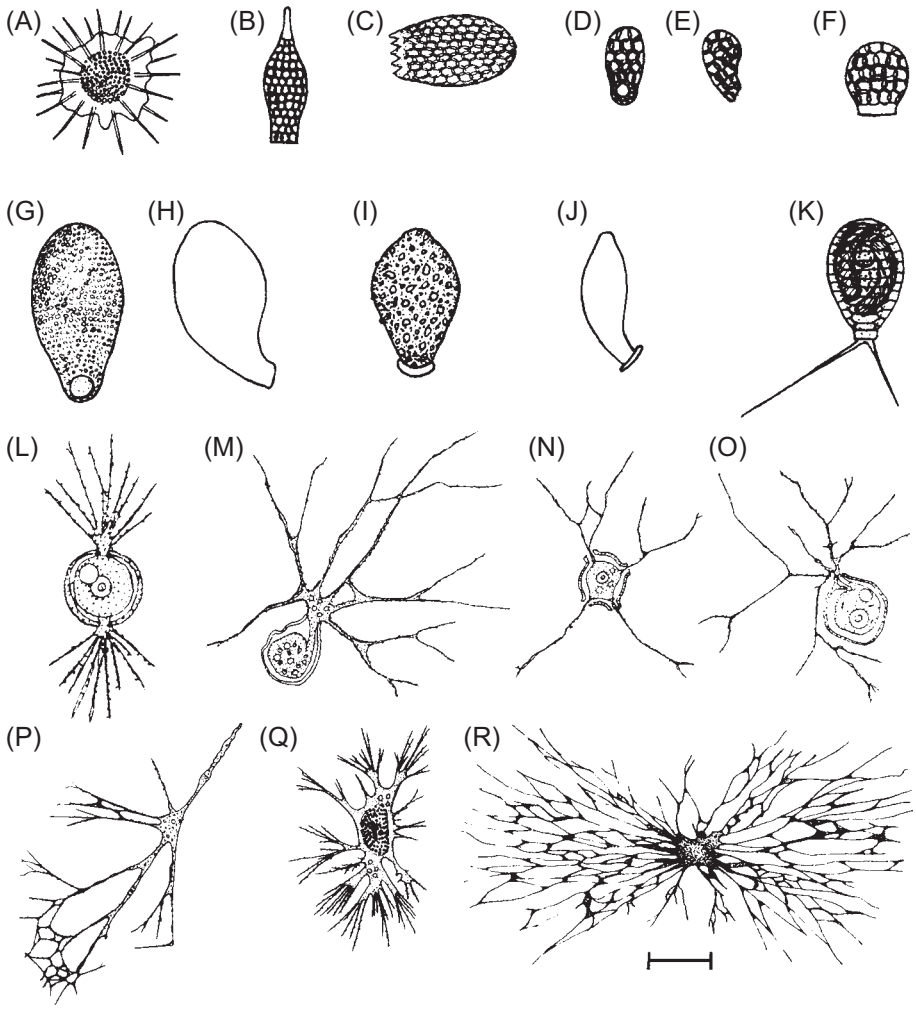


FIGURE 2.6 (A) *Vampyrella lateritia*; (B) *Paraeuglypha reticulata*; (C) *Euglypha tuberculata*; (D and E) *Trinema enchelys*, oral and side views; (F) *Sphenoderia lenta*; (G and H) *Cyphoderia ampulla*; (I and J) *Campascus triqueter*; (K) *Paulinella chromatophora*; (L) *Diplophyrys archeri*; (M) *Liekerkuehnia wagnerella*; (N) *Microcometes paludosa*; (O) *Microgromia haeckeliana;* (P) *Biomyxa vegans*; (Q) *Chlamydomyxa montana*; (R) *Reticulomyxa filosa. After: Bovee (1985) (B and D–R); Deflandre (1959) (A and C). Scale 5–10 µm for (L, N, and O); 15 µm for (K); 25 µm for (A–C); 40 µm for (D, F, and G); 50 µm for (I, M, and Q); 80 µm for (P); and 10,000 µm for (R).*

sequestering chloroplasts from ingested algae that are kept functional in the ciliate cytoplasm (Esteban et al. 2010).

Karyorelictea

The ciliates are divisible into 12 classes (Adl et al., 2012). Members of the class Karyorelictea are thought primitive for the group, with numerous nondividing macronuclei that are not highly polyploid. They are largely benthic, the best-known freshwater example being *Loxodes* (Fig. 2.9 J). Compound ciliary organelles associated with the cytostome are prominent in the classes Heterotrichea and Spirotrichea. Large heterotrichs, such as *Stentor* and *Spirostomum* (Figs. 2.10 A, F), are familiar as teaching material. Spirotrichs are abundant in many freshwater habitats, from plankton (choreotrichs and oligotrichs, Figs. 2.11 S–W) to the benthos (e.g., many stichotrichs and hypotrichs). Stichotrichs and hypotrichs (Figs. 2.11 A–H, N–Q and 2.12 X, Y) are mostly dorsoventrally flattened crawlers with compound ciliary structures called cirri.

Nassophorea

The Nassophorea are named for their basket-like nasse or cyrtos supporting the cytopharynx (Figs. 2.12V, W, Z and 2.19 E, I). The armophoreans were formerly placed in the Heterotrichea but are now recognized as a separate class, Armophorea, established on the basis of small subunit (SSU) rRNA gene sequence data. Armophoreans are found only in anoxic habitats, benthic, pelagic, or as endosymbionts in the digestive systems mainly of invertebrates. Armophoreans are free-swimming, typically small to

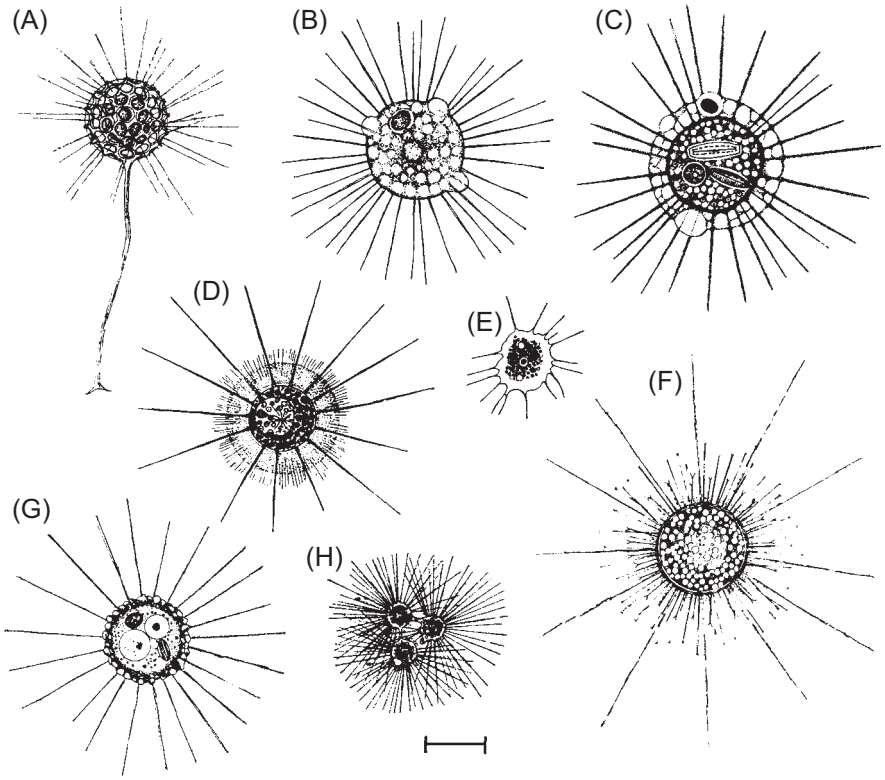


FIGURE 2.7 (A) *Clathrulina elegans*; (B) *Actinophrys sol*; (C) *Actinosphaerium eichhorni*; (D) *Heterophrys myriopoda*; (E) *Ciliophrys infusorium*; (F) *Acanthocystis turfacea*; (G) *Lithocolla globosa*; (H) *Raphidiophrys elegans*. *After: Deflandre (1959) (H); Kudo (1966) (B–E); Rainer (1968) (A, F, and G). Scale 15 μm for (E); 30 μm for (B, D, and G); 50 μm for (A); 75 μm for (F and H); and 160 μm for (C).*

medium size, with multiple adoral polykinetids and a somatic ciliature that is typically holotrichous but sometimes reduced (Figs. 2.11 K, R).

Prostomatea and Litostomatea

Classes Prostomatea (Figs. 2.10 J, O) and Litostomatea (Figs. 2.9 D, E, H and 2.13 J, M) are largely predators, often of other ciliates. Prostomes generally have apical cytostomes, while many litostomes have subapical, sometimes slit-like cytostomes. The mouth is encircled by a crown of cilia from whose bases (kinetosomes) arise the rhabdos, a cylinder of microtubules surrounding and supporting the cytopharynx. Toxicysts are found in most species and are used to subdue active prey. Toxicysts may be found around the cytostome, on a proboscis, on tentacles, or elsewhere on the body. A number of short, specialized kineties (rows of kinetosomes) are often found near the anterior. This brosse (brush) probably assists in prey recognition.

Phyllopharyngea

This class contains the distinctive Suctoria (Figs. 2.13 B–F, I, 2.14, 2.15 A–C, 2.16 B, C, J, L and 2.19 D), sessile or free-floating predators of other ciliates. Suctoria are unusual in that most have several "sticky" feeding tentacles rather than a single mouth. Suctoria reproduce by unequal binary fission (budding), which yields a ciliated dispersal stage or "swarmer." Other groups within the Phyllopharyngea include the Cyrtophoria, which contains surface-associated algivores such as *Chilodonella* (Fig. 2.17 T) and *Chlamydodon* (Fig. 2.19 F), plus a diverse array of epizooic and free-living forms such as chonotrichians and rhynchodians (Gong et al., 2009).

Colpodea

Colpodeans (Figs. 2.16 F, G, M, 2.17 K, L, N, P–S and 2.18 G) are not common in freshwater environments, most being terrestrial bacterivores. They are more likely to be encountered in small, temporary waters. Plagiopylea is a riboclass whose monophyly, like the class Armophorea, is based only on the evidence of sequences of the SSU rRNA gene. Also like the armophoreans, plagiopyleans are considered to be anaerobic or microaerophilic and include groups not formerly thought to be phylogenetically related, e.g., the "classic" plagiopyleans (Fig. 2.17 M), which were

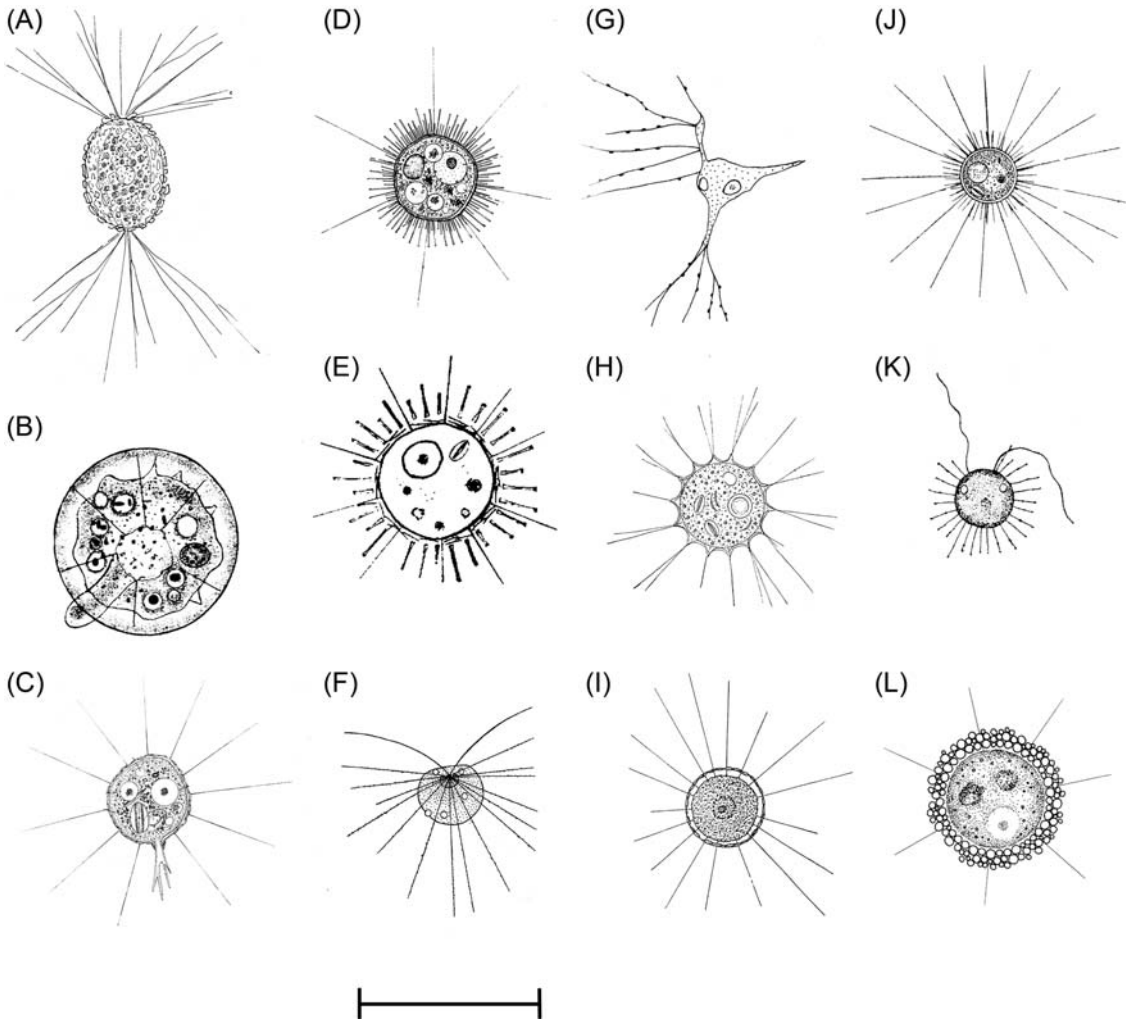


FIGURE 2.8 (A) *Amphitrema stenostoma*; (B) *Microchlamys patella*; (C and I) *Pinaciophora fluviatilis*; (D) *Rabdiophrys anulifera*; (E) *Rabdiaster pertzovi*; (F) *Heliomorpha depressa*; (G) *Limnofila mynlikovi*; (H) *Clathrella foreli*; (J) *Acanthoperla ludibunda*; (K) *Heliomorpha depressa*; (L) *Acinetactis mirabilis*; (M) *Pompholyxophrys punicea*. *After Greef (1869) (I); From Siemensma, Ferry J.; Page, F. C., Nackte rhizopoda und heliozoea, 1991. (L); Mikrjukov (1999) (J); Mikrjukov (2001) (E); Mikrjukov and Mylnikov (1995) (called* Penardia cometa*) (G); Penard (1902) (A and B); Penard (1905) (H); Rainer (1968) (C and D); Schoutenden (1907) (F and K); Siemensma (1991) (M). Scale = 200 μm (C and I); 100 μm D; 50 μm (A, B, G, H, and J–M); 25 μm (E and F).*

formerly placed in the Colpodea and resemble colpodids in form, and the odontostomes (Figs. 2.11 J, M). Recently another anoxic ciliate lineage that was initially known only from marine environmental rRNA sequence data has been characterized, based on which the class Cariacotrichea was established (Orsi et al., 2011).

Oligohymenophorea

Members of the Oligohymenophorea are mostly microphagous, and this class is named for the compound ciliary organelles that are found in a buccal cavity surrounding the cytostome. The most common pattern (in subclasses Hymenostomatia, Scuticociliatia, and Peniculia; Figs. 2.9 L–X, 2.15 H, I, 2.17 A–J and 2.19 G) is three polykinetids on the left side of the buccal cavity and an undulating membrane on the right. The net result is three brushes, the polykinetids, working against a curved wall, the undulating membrane, to deliver small particles to the cytostome. The large subclass Peritrichia (Figs. 2.12 A–U, 2.13 H, 2.18 I and 2.19 H) contains sessile bacterivores in which the buccal cavity is deepened as an infundibulum, and the polykinetids wind down it to the cytostome after encircling a prominent peristome. Somatic ciliature is absent in most

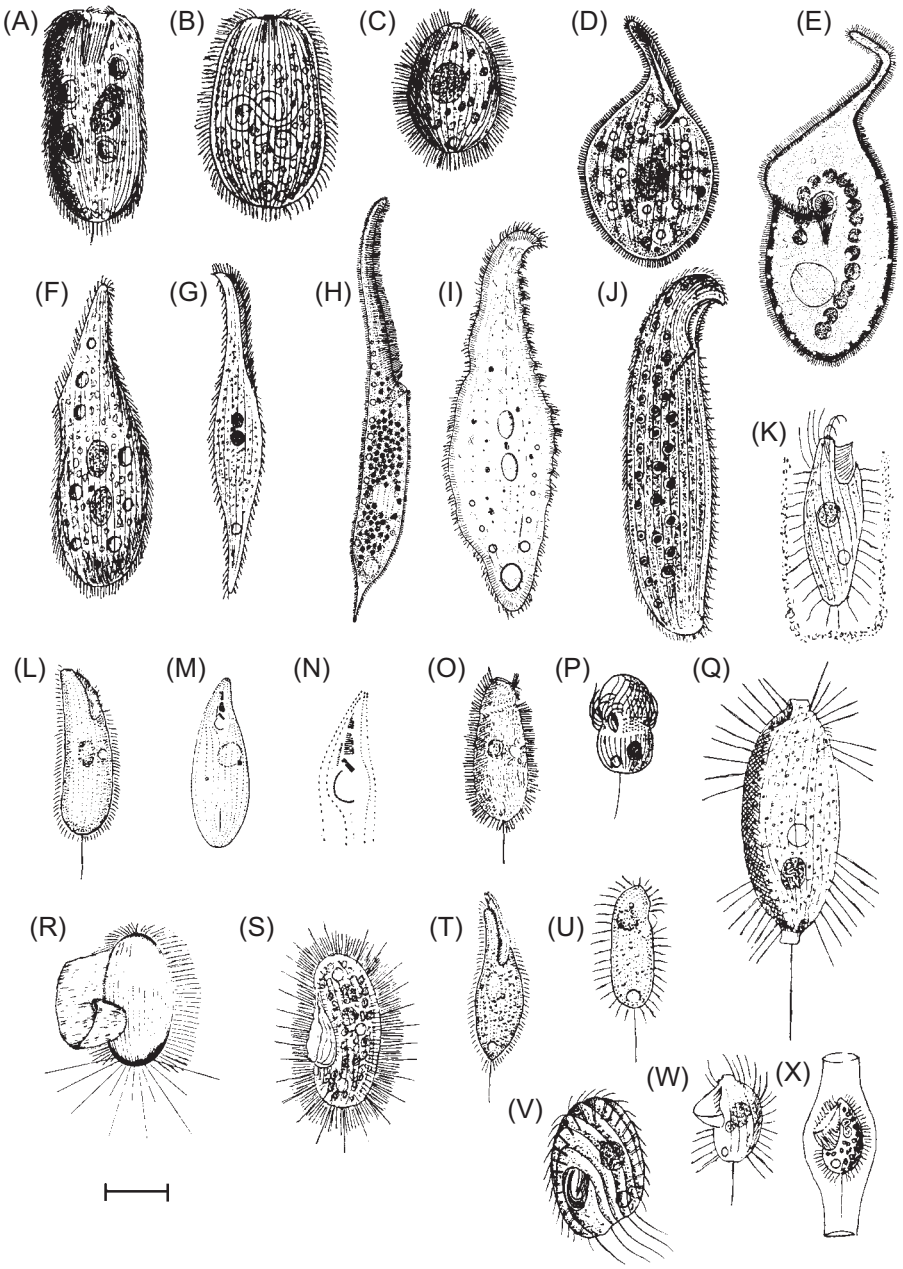


FIGURE 2.9 (A) *Prorodon teres*; (B) *Pseudoprorodon ellipticus*; (C) *Holophyra simplex*; (D) *Trachelius ovum*; (E) *Paradileptus robustus*; (F) *Amphileptus claparedi*; (G) *Litonotus fascicola*; (H) *Dileptus anser*; (I) *Loxophyllum helus*; (J) *Loxodes magnus*; (K) *Cyrtolophosis mucicola*; (L–N) *Philasterides armata*, live, silver-stained, and oral detail of silver-stained specimen; (O) *Loxocephalus plagius*; (P) *Urozona bütschlii*; (Q) *Balanonema biceps*; (R) *Pleuronema coronatum*; (S) *Histiobalantium natans*; (T) *Cohnilembus pusillus*; (U) *Uronema griseolum*; (V) *Cinetochilum margaritaceum;* (W) *Cyclidum glaucoma*; (X) *Calyptotricha pleuronemodies*. *After: Corliss (1979) (R); Dragesco (1966a) (I); Grolière (1980) (M and N); Kahl (1930–1935) (A–C, F, G, J, K, O–Q, S, and V–X); Kudo (1966) (I); Noland (1959) (L, T, and U). Scale 10 μm for (K); 15 μm for (P and V); 20 μm for (T, U, W, and X); 25 μm for (G, H, L, and M); 30 μm for (C, I, and S); 40 μm for (B and R); 50 μm for (F); 60 μm for (A and O); and 75 μm for (D, E, and J).*

species. Many are attached to the substrate by a stalk, as in the common *Vorticella* (Fig. 2.12 K), and a few are secondarily free-swimming. Peritrichs may be either solitary or colonial. For a comprehensive treatment of the taxonomy of ciliates, see Lynn (2008).

MATERIAL PREPARATION AND PRESERVATION

To identify certain species of protozoa, it may be necessary to cultivate them. This involves isolating them from other

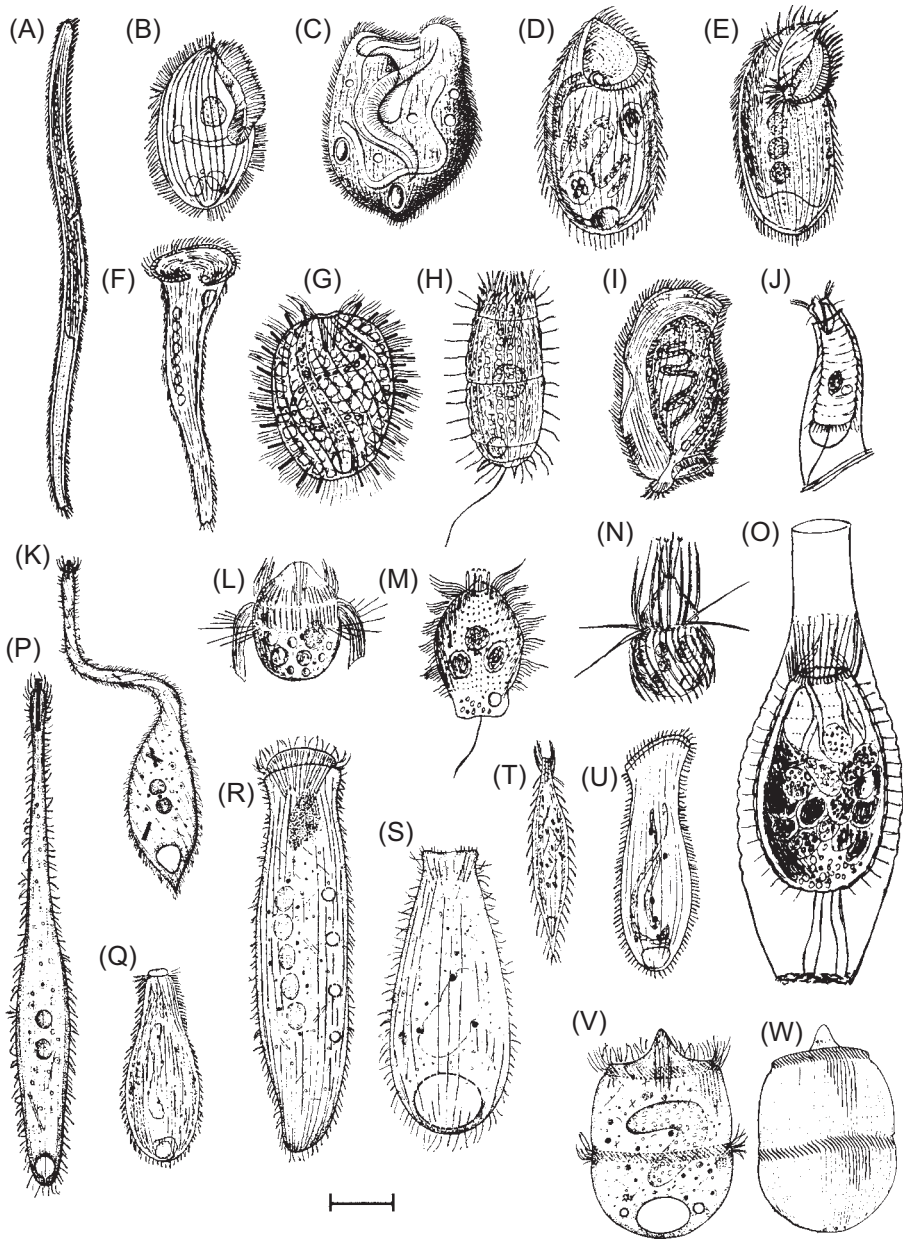


FIGURE 2.10 (A) *Spirostomum minus*; (B) *Blepharisma lateritium*; (C) *Bursaria truncatella*; (D) *Climacostomum virens*; (E) *Condylostoma tardum*; (F) *Stentor polymorphus*, half extended; (G) *Actinobolina radians*; (H) *Coleps hirtus*; (I) *Bryophyllum lieberkühni*; (J) *Metacystis recurva*; (K) *Lacrymaria olor*; (L) *Askenasia volvox*; (M) *Urotricha farcta*; (N) *Mesodinium pulex*; (O) *Vasicola ciliata*; (P) *Trachelophyllum apiculatum*; (Q) *Enchelyodon elegans*; (R) *Homalozoon vermiculare*; (S) *Enchelys simplex*; (T) *Chaenea teres*; (U) *Spathidium spathula*; (V and W) *Didinium nasutum*, live and silver-stained. *After: Dragesco (1966a) (K, S, V, and W); Dragesco (1966b) (P and R); Kahl (1930–1935) (A, B, D–J, L–O, Q, T, and U); Kent (1882) (C). Scale 10 µm for (M and N); 20 µm for (H, J, L, P, and S); 30 µm for (G, O, and U); 40 µm for (B, K, and T); 60 µm for (E, Q, and R); 80 µm for (D, V, and W); 100 µm for (A, F, and I); and 200 µm for (C).*

(contaminant) organisms and then growing them in a culture medium. In general, all initial manipulations and transfers should be performed where possible in media with pH and osmotic potential similar to those at the site of isolation. Likewise, it is optimal that suitable temperature, light, and oxygen tension regimes should also be maintained throughout the isolation and culturing processes. Numerous methods for the isolation and cultivation of protozoa have been reported, and these have been reviewed or summarized on a number of occasions (Finlay et al., 1988; Kirsop & Doyle, 1991; Lee & Soldo, 1992; Nerad, 1993; Tompkins et al., 1995; Day et al, 2007).

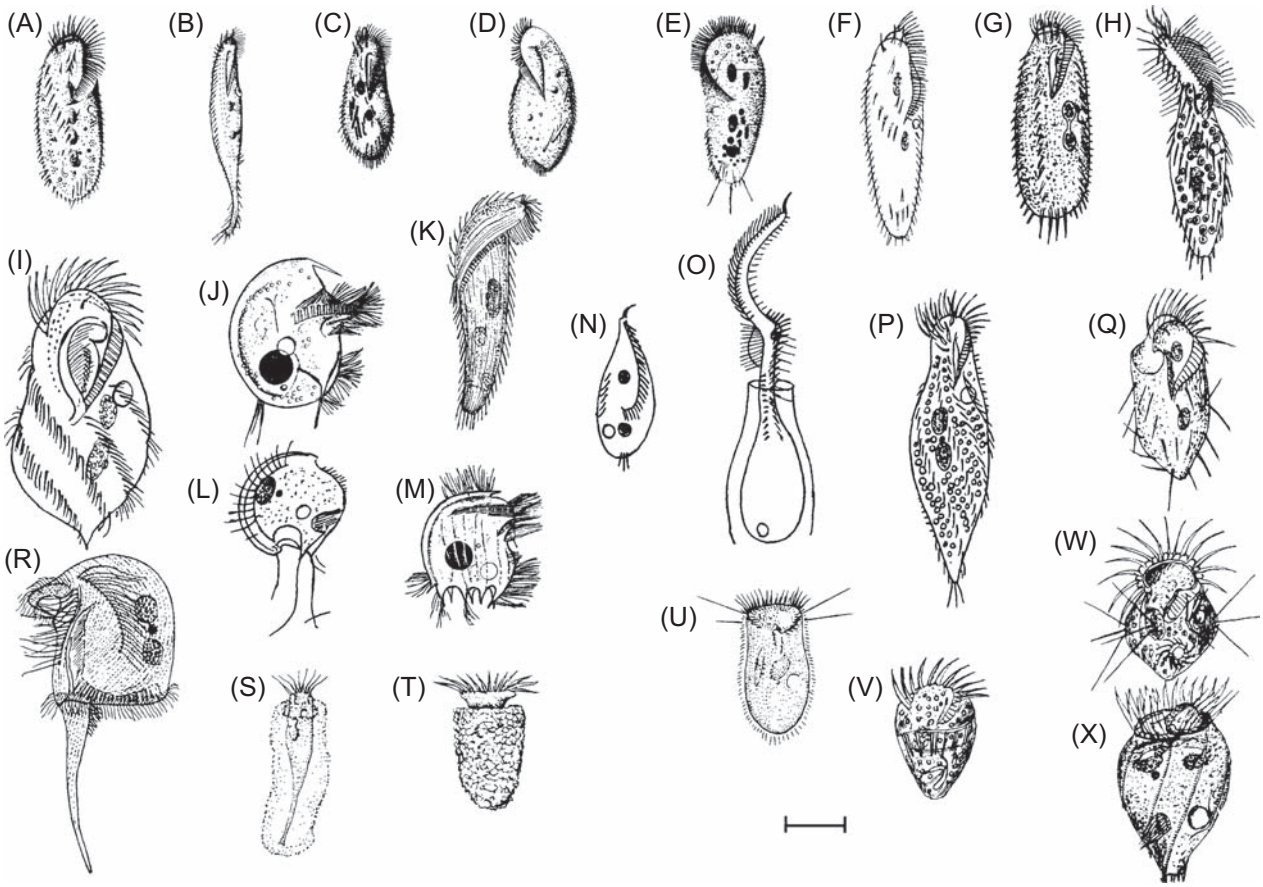


FIGURE 2.11 (A) *Gastrostyla steini*; (B) *Uroleptus piscis*; (C) *Oxytricha fallax*; (D) *Urostyla grandis*; (E) *Stylonychia mytilus*; (F) *Gonostomum affine*; (G) *Amphisiella oblonga*; (H) *Stichotricha aculeata*; (I) *Hypotrichidium conicum*; (J) *Discomorphella pectinata*; (K) *Metopus es*; (L) *Myelostoma flagellatum*; (M) *Saprodinium dentatum*; (N and O) *Chaetospira müller*i, contracted and extended forms; (P) *Strongylidium crassum*; (Q) *Psilotricha acuminata*; (R) *Caenomorpha medusula*; (S) *Tintinnidium fluviatile*; (T) *Tintinnopsis cylindricum;* (U) *Strombidinopsis setigera*; (V) *Strombidium viride*; (W) *Halteria grandinell*a; (X) *Strobilidium gyrans*. *After: Jankowski (1964a,b) (J and M); Kahl (1930–1935) (F–I, K, L, N–R, and V–X); Kent (1882) (A–E); Noland (1959) (S–U). Scale 15 μm for L; 20 μm for (A, B, G, and P); 25 μm for (H, W, and X); 30 μm for (F, I, J, P–R, and T); 40 μm for (G, K, M–O, S, U, and V); 60 μm for (B); 80 m for (A and C); and 140 μm for (D).*

Methods to collect protozoa are described in Volume I's chapter on protozoa, but following we describe more detailed methods for isolating, culturing, and preserving selected groups.

Isolation

There is a wide variety of methods of isolation, and these can broadly be classified into three categories: enrichment methods, dilution methods, and physical methods. Enrichment is the inoculation of a field sample into an equal or greater volume of suitable medium and incubation under favorable conditions. By inoculation of parallel cultures in a range of media, different organisms will be selected. For bacterivorous protozoa, the simplest way to enrich a sample is to add boiled grains of barley, wheat, or rice, which will promote the growth of bacteria and thereby produce a food source for the protozoa. Some commonly used enrichment methods are described in Finlay et al. (1988) and Lee & Soldo (1992). The development of bacterivores may also encourage the growth of carnivorous protozoa that will feed upon them. Dilution methods are most effective for use on preponderantly uniprotozoan samples. Material is sequentially diluted in an appropriate medium and incubated under favorable conditions. The greatest dilution in which growth occurs is likely to be uniprotozoan and usually isolates the most abundant species in a sample. Details of various dilution methods are described in Cowling (1991) and Finlay et al. (2000). Once isolated, it may be important to reduce the volume of liquid in which the cell is contained. Physical methods involve the selection of individual protozoan cells and their transfer into a growth medium. Micropipetting with thin capillary pipettes, working under a dissecting microscope, can be

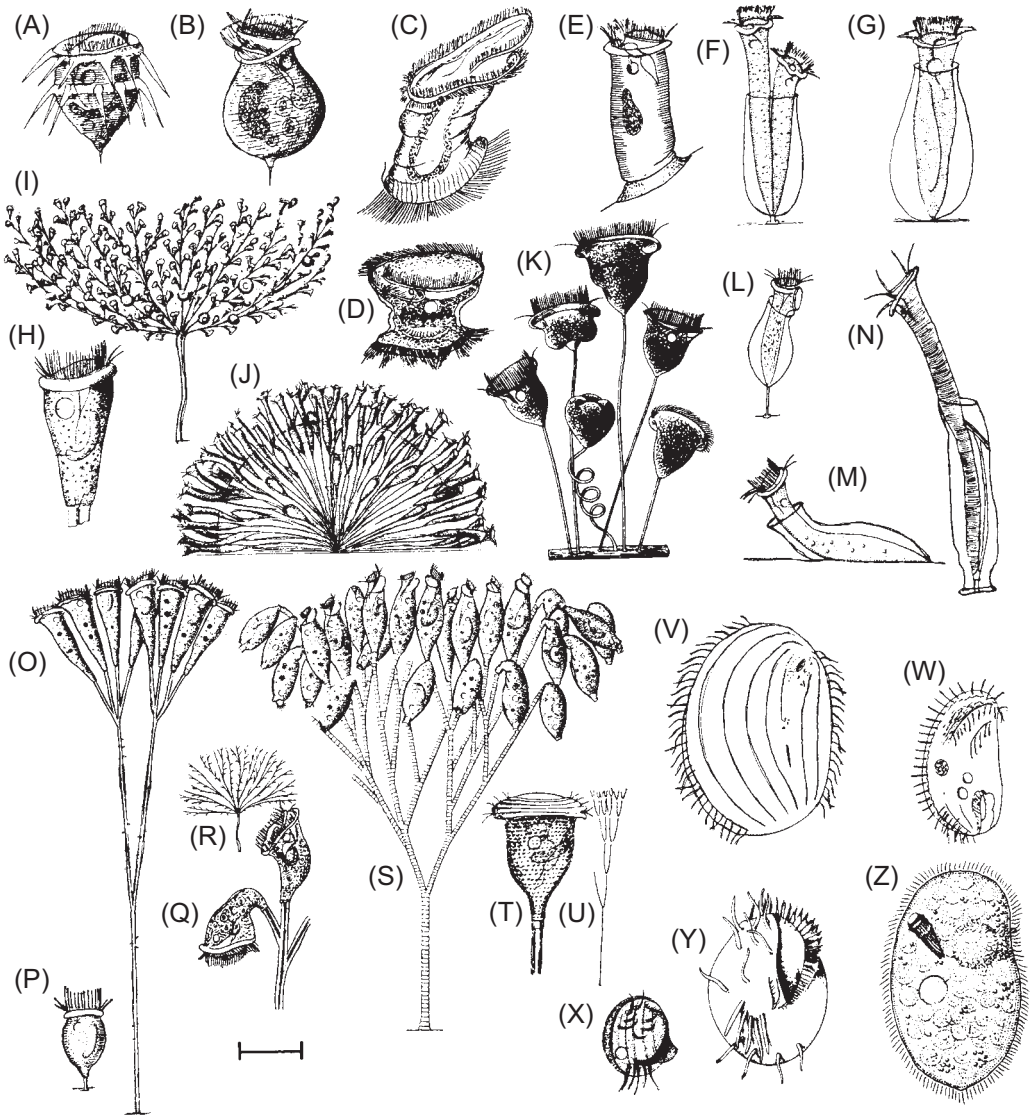


FIGURE 2.12 (A) *Hastatella radians*; (B) *Astylozoon faurei*; (C) *Urceolaria mitra*; (D) *Trichodina pediculis*; (E) *Scyphidia physarum*; (F) *Cothurnia imberbis*; (G) *Vaginicola ingenita;* (H and I) *Zoothamnium arbuscula*, individual and colony; (J) *Ophrydium eichhorni*; (K) *Vorticella campula*; (L) *Pyxicola affinis*; (M) *Platycola longicollis*; (N) *Thuricola folliculata*; (O) *Epistylis plicatilis*; (P) *Rhabdostyla pyriformis*; (Q and R) *Carchesium polypinum*, individual and colony; (S) *Opercularia mutans*; (T and U) *Campanella umbellaria*, individual and colony; (V) *Pseudomicrothorax agilis*; (W) *Microthorax pusillus*; (X) *Aspidisca costata*; (Y) *Euplotes patella*; (Z) *Nassula ornata. After: Corliss (1979) (V and Y); Kahl (1930–1935) (A–E, H, L, N, Q, R, T, U, and W); Kent (1882) (I–K, O, S, and X); Noland (1959) (F, G, M, and P). Scale 15 µm for (V and W); 20 µm for (A, B, G and P); 25 µm for (D, H, F, and X); 30 µm for (C and Z); 40 µm for (E, L, M, N, and S); 50 µm for (O); 75 µm for (K, Q, and I); and 200 µm for (J).*

used for a wide variety of protozoa, particularly those that are relatively large and/or slow. Other methods of isolation include silicone oil plating, flow cytometry, agar plating, and electromigration. Silicone oil plating involves the isolation of clone-founding cells within microdroplets formed from vortex-mixed oil/culture emulsions (Soldo & Brickson, 1980). Flow cytometry is an automated means of discriminatory cell sorting and isolation on the basis of various cell attributes, including size and density. It is particularly useful for cells that contain pigments that give a fluorescent signal and has also been applied successfully to isolate protozoa using their fluorescent food vacuole contents (Keenan et al., 1978). Agar plating methods rely on discerning colony growth of isolated clones on agar surfaces or within agar, and are particularly useful for amoebae and some flagellates. Usually one or two drops of sample are placed onto a nonnutrient agar plate that has been streaked with a suitable food organism, and then incubated. Amoebae then migrate across the agar surface away from site of inoculation, thereby isolating themselves

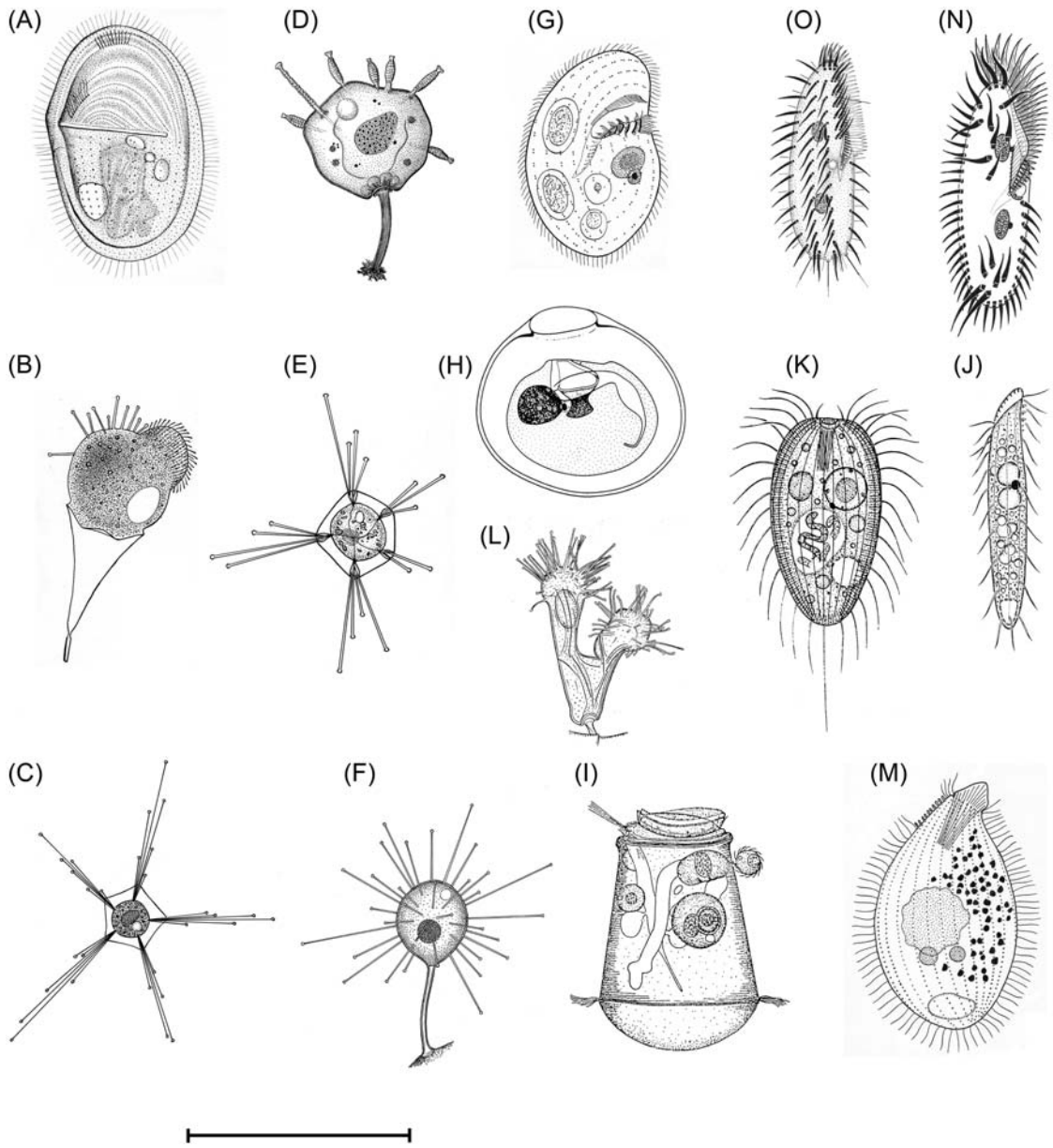


FIGURE 2.13 (A) *Gastronauta* sp; (B) *Paracineta patula*; (C) *Metacineta micraster* var. *pentagonalis* (called *M. pentagonalis* in Nozawa, 1939); (D) *Choanophrya infundibulifera*; (E) *Solenophrya micraster*; (F) *Prodiscophrya collini*; (G) *Bryometopus pseudochilodon*; (H) *Usconophrys aperta*; (I) *Endosphaera engelmanni* in cytoplasm of *Opisthonecta henneguyi*; (J) *Apertospathula armata*; (K) *Apsikrata gracilis*; (L) *Lecanophryella paraleptastaci*; (M) *Lagynophrya fusidens*; (N) *Trachelostyla ciliophorum*; (O) *Wallackia schiffmanni*. *After Clamp (1991) (H); Curds (1982) (A–F and M); Curds et al. (1983) (G, N, and O); Dovgal (1985) (L); Foissner & Xu (2006) (J); Foissner (1984) (K); Matthes (1971) (I). Scale = 200 μm (C and I); 100 μm (E and O); 50 μm (A, G, H, J, and K–N); 25 μm (D and F).*

from other organisms in the sample. The amoebae may then be picked off and subcultured (Lee & Soldo, 1992; Day et al., 2007). Electromigration is a method for obtaining concentrated suspensions of ciliated and flagellated protozoa relatively free of bacteria and other organisms. It works on the principle that many ciliates and flagellates orient themselves in a direct current and migrate toward the cathode (Schmidt, 1982). It is particularly useful for the isolation of organisms from mud and sediment samples.

Cultivation

To maintain cultures of protozoa long term, it is necessary to provide a medium that suits each species and a supply of

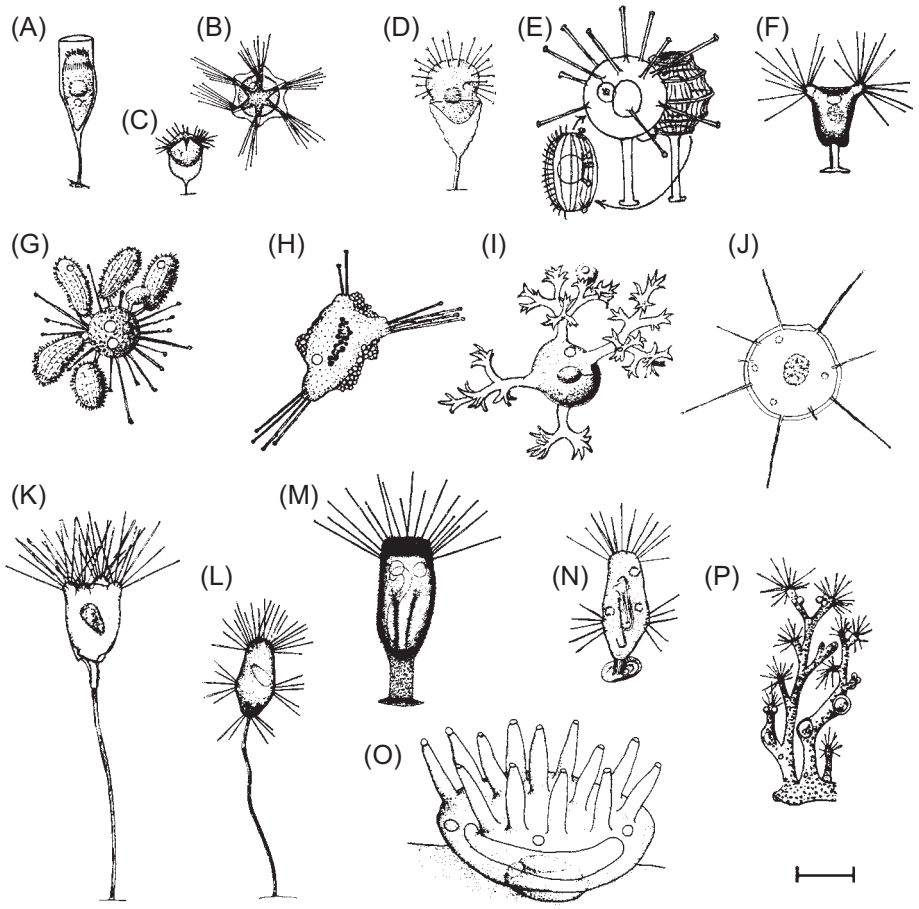


FIGURE 2.14 (A) *Thecacineta cothurniodes*; (B and C) *Metacineta mystacina*, top and side views; (D) *Paracineta crenata*; (E) *Podophrya fixa*, showing trophont, encysted form, and swarmer; (F) *Acineta limnetis*; (G) *Sphaerophyra magna*; (H) *Trichophyra epsitylidis*; (I) *Dendrocometes paradoxus*; (J) *Heliophrya reideri*; (K) *Tokophrya quadripartita*; (L) *Multifasciculatum elegans*; (M) *Squalorophyra macrostyla*; (N) *Discophrya elongata*; (O) *Stylocometes digitalis*; (P) *Dendrosoma radians*. *After: Corliss (1979) (P); Goodrich and Jahn (1943) (F, K, L, and M); Kent (1882) (G and I); Matthes (1954) (J and O); Noland (1959) (A–D and N); Small and Lynn (2000) (E and H). Scale 15 μm for (E, H, J, and O); 30 μm for (A, D, F, and G); 50 μm for (I and L–N); 75 μm for (B and K); and 2000 μm for (P).*

appropriate food. Various publications provide comprehensive information or refer to media preparations for protozoa (Kirsop & Doyle, 1991; Lee & Soldo, 1992; Nerad, 1993; Tompkins et al., 1995; Finlay et al., 2000; Day et al., 2007). However, certain isolation techniques, growth media, and culture conditions suit a wide range of organisms. Some of these are discussed following.

The methods for the cultivation of flagellates and ciliates are often identical or similar, so these two groups will be dealt with together and the amoebae separately. The choice of culture medium will depend largely upon the natural protozoan diet. Many flagellates and ciliates eat bacteria; and in these cases, nonselective media, designed for the growth of bacterial populations, may be used. For many species, isolates may be cultured in the presence of mixed bacterial flora that coexisted with the target organism in its original habitat. Alternatively, selective cultures may be obtained by incubating the protozoa in an inorganic salt solution along with an appropriate food organism. In some cases, nonpathogenic laboratory cultures of bacteria may be used, whereas in others it may be necessary to isolate bacteria from the original sample and use one or more of these strains as the selected food organisms. For omnivores and carnivores, an examination of the contents of the food vacuoles may give an indication of the preferred food. The organism can then be incubated in the presence of its natural prey. In some cases it may be necessary to carry out replicated feeding experiments using a range of food organisms to determine which will support the growth of the isolate.

Culture media may be categorized into four main types: plant infusions, soil extract-based media, inorganic salt solutions, and specific (organically rich) media. Plant infusions are commonly used for bacterivorous flagellates and ciliates. The principle is that organic compounds leach out of plant material, and these support bacterial growth.

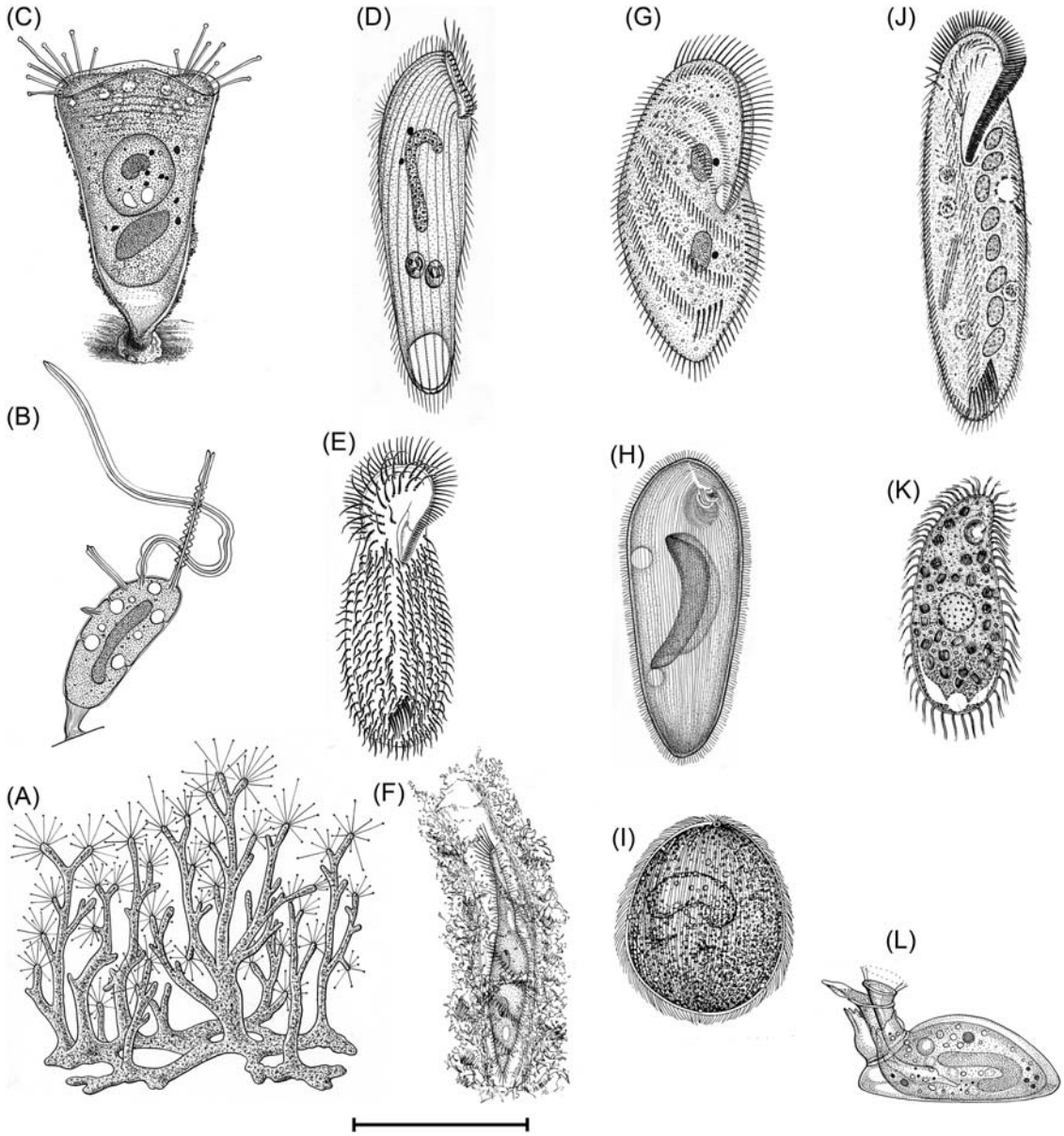


FIGURE 2.15 (A) *Dendrosoma radians*; (B) *Rhynchophrya palpans*; (C) *Periacineta linguifera*; (D) *Rheichenowella nigricans*; (E) *Pseudourostyla levis*; (F) *Stichotricha* sp.; (G) *Kerona pediculus*; (H) *Ophryoglena rhabdocaryon*; (I) *Ichthiophthirius multifiliis*; (J) *Pseudokeronopsis similis*; (K) *Parabryophrya penardi;* (L) *Lagenophrys nassa. After Corliss (1979) (I); Curds (1982) (A–F); Curds et al. (1983) (G, H, and L); Shi et al. (2007) (J); Foissner (1985) (K). Scale = 200 μm (B, C, and I); 100 μm (E and K); 50 μm (A, G, H, J, and L); 25 μm (D and F).*

The most commonly used are lettuce, hay, powdered cereal leaf, and grains of rice, wheat, and barley. Soil extract media are similar to plant infusions in the sense that organic compounds that will support the growth of bacteria are extracted from the soil. Thus, these media may also be used for the cultivation of bacterivorous species. Inorganic salt solutions provide a balanced medium for the growth of many protozoa. However, they contain negligible quantities of organic matter, so the addition of food organisms, or a carbon source, is essential. Such media are commonly used for the cultivation of carnivorous species. Specific, defined media may be used for producing axenic cultures. Such media invariably contain high concentrations of dissolved organic compounds, usually derived from animal sources. Optimal maintenance conditions (e.g., temperature, pH, oxygen tension) and the frequency of subculturing may be highly variable among different species and should usually take account of the conditions in the natural habitat and the feeding strategy of the isolate. For example, algivorous species should be kept in conditions of illumination that

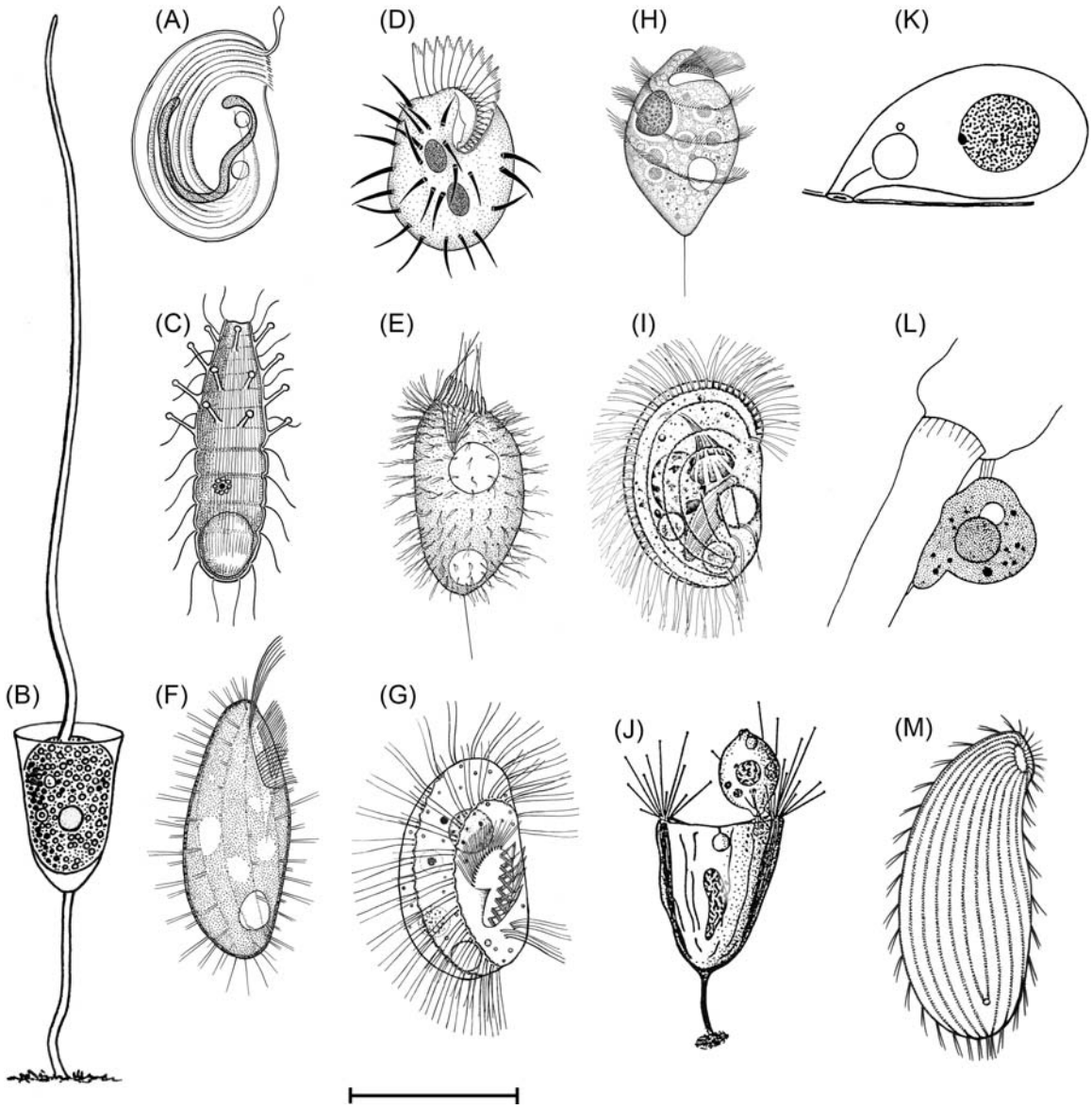


FIGURE 2.16 (A) *Lophophorina capronata*; (B) *Acinetopsis elegans*; (C) *Encelyomorpha vermicularis*; (D) *Psilotricha viridis*; (E) *Plagiocampa ovata*; (F) *Cyrtolophosos mucicola*; (G) *Kreyella minuta*; (H) *Trimyema compressum*; (I) *Pseudochlamydonella rheophyla*; (J) *Pseudogemma pachystyla* (trophont on *Acineta tuberosa*); (K) *Trypanococcus rotiferorum*; (L) *Manuelophrya parasitica*; (M) *Woodfruffia spumacola. After Batisse (1968) (J); Batisse (1994) (K); Curds (1982) (A–C, F–H, and M); Curds et al. (1983) (D and E); Foissner (1993) (I); Matthes (1988) (L). Scale = 40 μm (B, D, H, J, and M); 30 μm (A and E); 20 μm (C and K); 15 μm (G, F, and I).*

allow an adequate algal food supply to be maintained, whereas bacterivorous and carnivorous species may best be cultivated in the dark in order to control algal contaminants.

Amoebae may be cultured in liquid media, on agar, or in biphasic media. Generally the larger forms are grown in liquid culture and the smaller forms on agar. In most cases, amoebae can be cultivated on a nonnutrient medium (liquid or agar) with a suitable bacterial food organism, although the medium can be enriched to stimulate growth of the bacterial food. Cultures of bacterivores should normally be cultivated in the dark, whereas algivorous amoebae, or those with algal symbionts, will require a light-dark cycle. Testate amoebae are often maintained on cereal leaf agar overlaid with a cereal leaf infusion. Details of media formulations and culture methods may be found in (Lee & Soldo, 1992; Nerad, 1993; Tompkins et al., 1995; Finlay et al., 2000; Day et al., 2007).

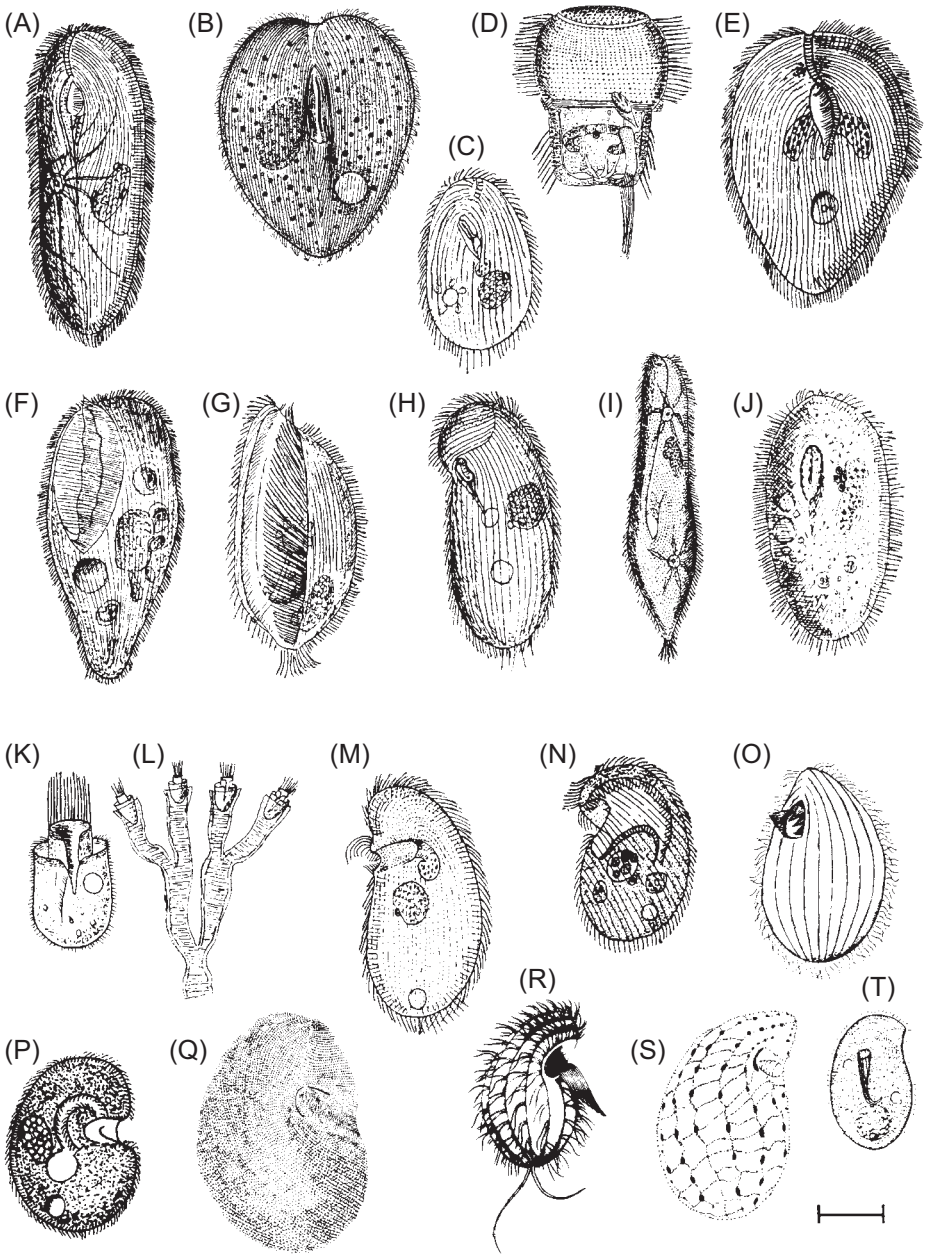


FIGURE 2.17 (A) *Frontonia leucas*; (B) *Stokesia vernalis*; (C) *Glaucoma scintillans*; (D) *Urocentrum turbo*; (E) *Parastokesia bütschlii* (called *Dismatostoma bütschlii)*; (F) *Turaniella vitrea*; (G) *Lembadion magnum*; (H) *Colpidium colpoda*; (I) *Paramecium caudatum*; (J) *Clathrostoma viminale*; (K and L) *Maryna socialis*, individual and colony; (M) *Plagiopyla nasuta*; (N) *Bresslaua vorax*; (O) *Tetrahymena pyriformis*; (P and Q) *Tillina magna*, live and line drawing of silver-stained specimen; (R and S) *Colpoda steini*, live and silver-stained; (T) *Chilodonella uncinata. After: Corliss (1979) (O and R); Dragesco (1966b) (B); Kahl (1930–1935) (A, C–M, and P); Kudo (1966) (N); Lynn (1976) (S); Lynn (1977) (Q); Noland (1959) (T). Scale 15 μm for (G, O, and R); 25 μm for (C and H); 30 μm for (D and F); 40 μm for (B, E, J, and M); 50 μm for (O); 60 μm for (I and N); and 75 μm for (A, K, and Q).*

Preservation

Wherever possible, protozoa should be observed *in vivo* to determine their behavior and certain features that may only be visible in live cells. Nevertheless, it may also be necessary to employ preservation methods, for example: (1) if it is not possible to observe the sample for a long period after collection; (2) to observe certain features not visible in live specimens; or (3) to maintain a reference collection of the organisms or permanent record of the sample. A useful general fixative is Lugol's iodine, 1%

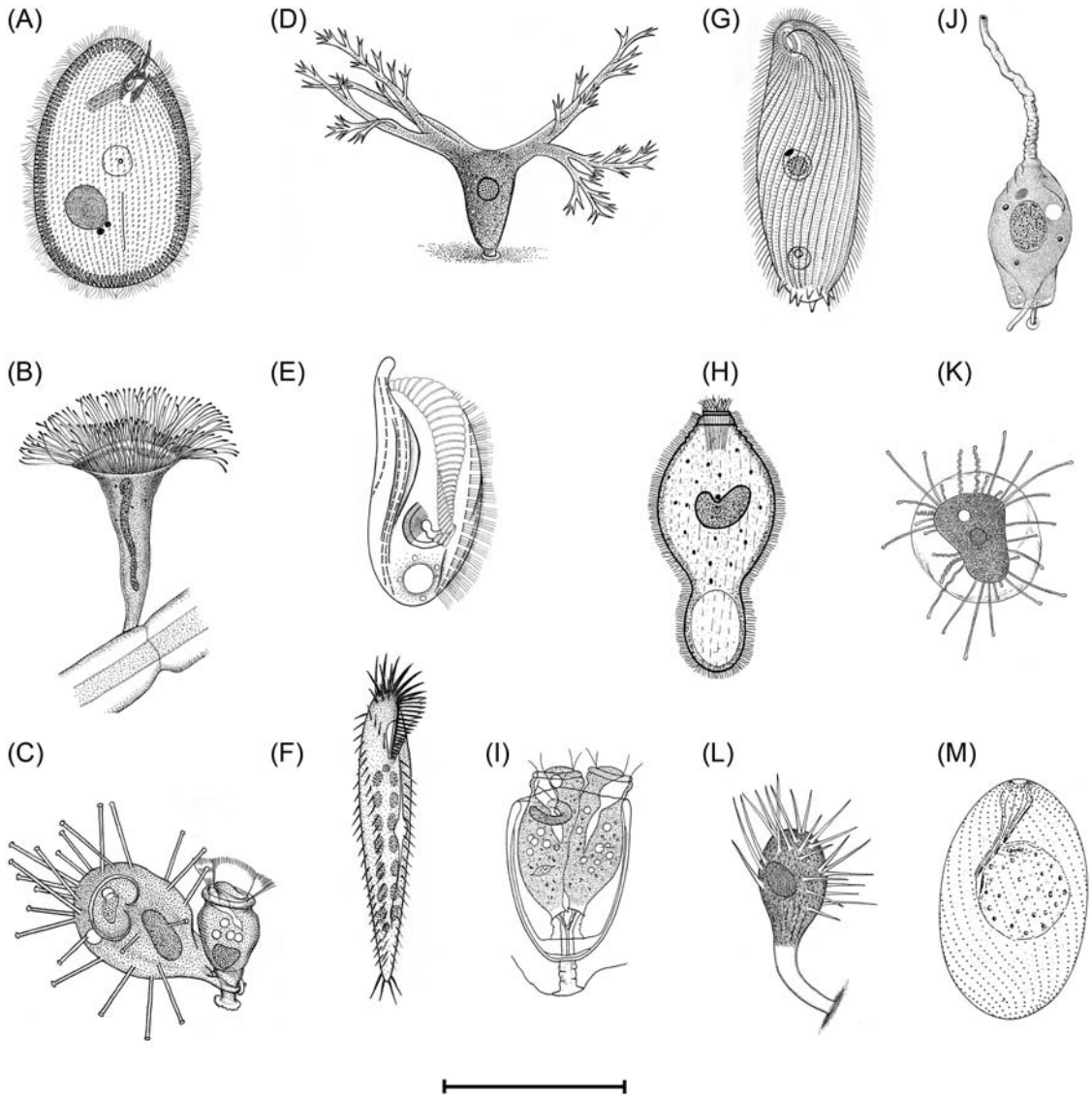


FIGURE 2.18 (A) *Furgasonia blochmanni*; (B) *Spelaeophrya troglocardis*; (C) *Erastophrya chattoni* (growing on the peritrich *Apiosoma*) (D) *Cometodendron eretum*; (E) *Phacodinium metchnicoffi*; (F) *Uroleptoides kihni*; (G) *Cirrophrya haptica*; (H) *Lagynus elegans*; (I) *Rovinjella sphaeromae*; (J) *Rhyncheta cyclopum*; (K) *Mucophrya pelagica*; (L) *Echinophrya horrida*; (M) *Pseudoholophrya terricola*. *After Berger et al. (1984) (M); Curds (1982) (A–F and J–L); Curds et al. (1983) (G); Dovgal (1985) (L); Matthes (1972) (I); Sola et al. (1990) (H). Scale = 200 µm (C and I); 100 µm (B and E); 50 µm (A, G, H, and J–L); 25 µm (D, F, and M).*

volume/volume, or higher in saline or hard water (Taylor & Heynen, 1987). Mercuric chloride has been used extensively but should probably be discontinued for safety and environmental reasons. These fixatives do not lend themselves to the identification of ciliates or to the detection of chromatophores in small flagellates. Filtration methods may aid with both of these problems. The quantitative protargol method or QPS (Montagnes & Lynn, 1987a,b; Skibbe, 1994) produces permanent, quantitative, stained preparations for identification of ciliates and flagellates, although it requires that samples be fixed in a concentrated Bouin's fixative. Various types of silver-staining techniques, which highlight ciliary patterns, have been used in the identification of ciliates (Lee et al., 1985; Foissner 1991). Other fixatives such as glutaraldehyde and/or osmium tetroxide (OsO_4) are used if cells are to be examined by electron microscopy. A comprehensive account many of the main commonly used methods for the collection, isolation, cultivation, and preservation of protozoa is given in Lee & Soldo (1992).

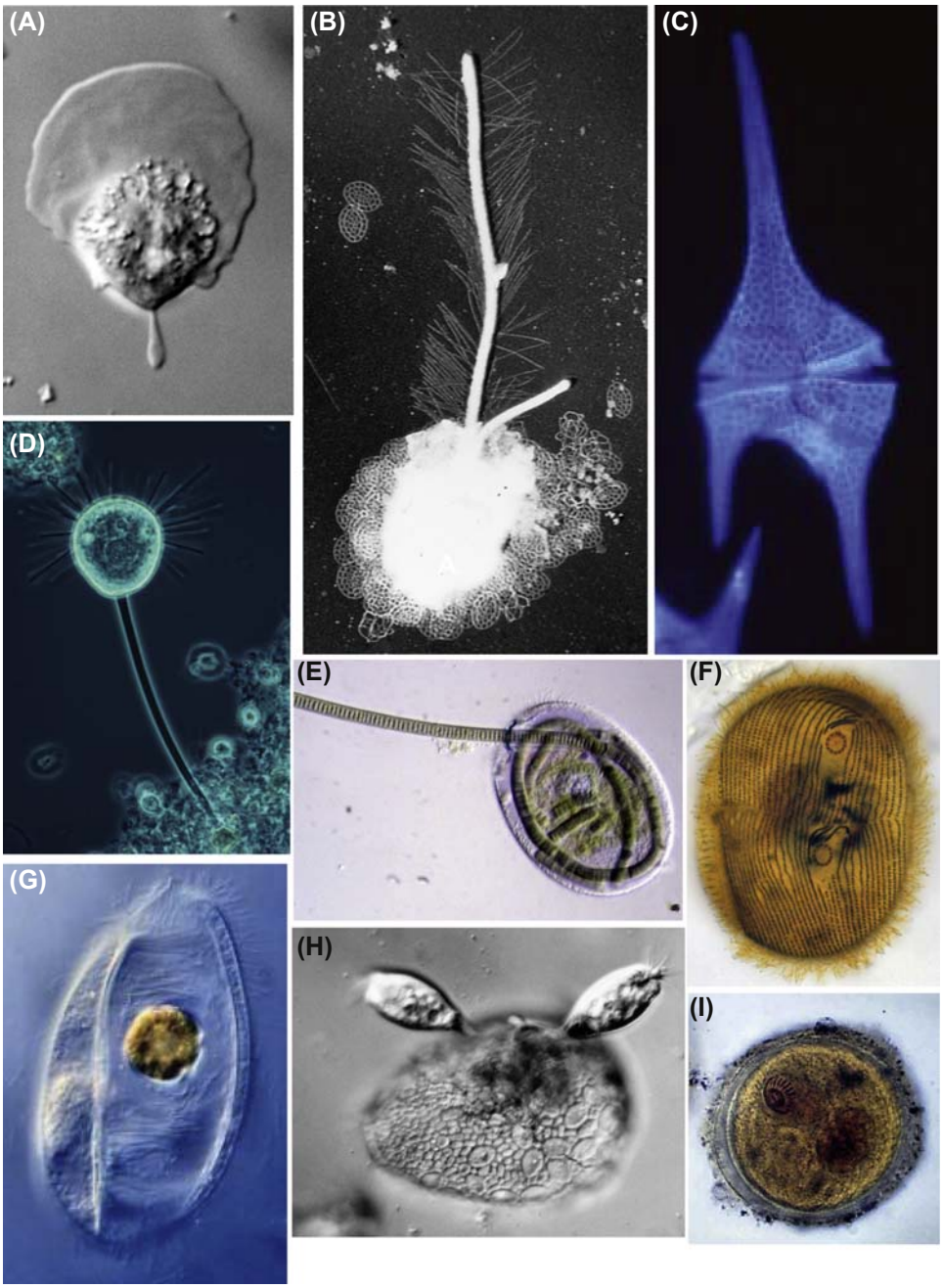


FIGURE 2.19 (A) naked amoeba; size: 50 µm across; (B) *Paraphysomonas butcheri* as seen under transmission electron microscopy, negative staining; size: 3 µm diameter (photograph courtesy of K. J. Clarke); (C) freshwater dinoflagellate, genus *Ceratium*; DAPI stained; size; 70 µm; (D) suctorian ciliate with tentacles radiating from the cell; size: 45 µm across; (E) ciliate *Nassula tumida* feeding on a filamentous cyanobacterium; cell size: 70 µm; (F) marine ciliate of the genus *Chlamydodon,* stained with silver to reveal the ciliary rows; this specimen is undergoing cell division (note the two circular mouths, one for each daughter cell); size; 150 µm; (G) ciliate *Lembadion magnum* catching a dinoflagellate; size: 80 µm; (H) testate amoeba with a colonial peritrichous ciliate attached to the test surface; size: amoeba 90 µm across, peritrichs 45 µm; and (I) dormant cyst of the ciliate *Nassula tumida*, shown in (E); note the denticulate circular mouth to the left of the image; size; 40 µm across.

ACKNOWLEDGMENTS

The contents of this chapter are based heavily on the chapter on protozoa by Bill Taylor and Bob Sanders in the third edition of *Ecology and Classification of North American Freshwater Invertebrates* (Thorp & Covich, 2010), which we have expanded and updated where necessary. We would therefore like to thank Bill and Bob for allowing us to use so much of their material and in doing so acknowledge their important contribution to this chapter.

KEYS TO PROTOZOA

Protozoa: Major Functional Groups

The phylum Cercozoa includes organisms that are amoeboid, flagellate, or both. This group is therefore included in the keys to both these major functional groups.

1 Flagella never or rarely present; primary organelles of locomotion and feeding are either pseudopodia or cilia 2

1′ Commonly 1–4 flagella (Fig. 2.1 A), 16–24 in one free-living genus (*Paramastix*) ..... **Flagellated protozoa**

2(1) Main organelles of locomotion and feeding are pseudopodia as in Figs. 2.1 B, C. Rarely, flagella may be present as well (e.g., Figs. 2.5 S–W and 2.6 A–I, K, P) ..... **Amoeboid protozoa**

2′ Simple cilia or compound ciliary organelles characteristic (but see Figs. 2.14 A–P) and present in at least one part of life cycle; subpellicular infraciliature present even when cilia are not; two types of nuclei (macronucleus and micronucleus) with rare exceptions (Fig. 2.1 D); ciliated protozoa..... phylum **Ciliophora**

Protozoa: Major Groups of Flagellated Protozoa

1 Without a median groove 2

1′ With median groove (annulus and sulcus); two flagella, one extending transversely around the cell (Fig. 2.3 A–C) ..... phylum Dinoflagellata

[Note: This group contains many or mostly photosynthetic members; several genera, however, have one or more species that lack chloroplasts and are thus heterotrophic, or contain chloroplasts but also exhibit heterotrophic nutrition.]

2(1) Without pharyngeal rods or paramylon as a reserve material 3

2′ Often large flagellates with pharyngeal rods (sometimes difficult to see) or containing the reserve material paramylon; one or usually two flagella arise from within an anterior invagination (reservoir); contractile vacuole associated with reservoir; elongate; body shape often plastic when living (Figs. 2.3 D, F–I) ..... phylum Euglenida

[Note: This group contains many or mostly photosynthetic members; several genera, however, have one or more species that lack chloroplasts and are thus heterotrophic, or contain chloroplasts but also exhibit heterotrophic nutrition.]

3(2) Cell with 1–4 flagella (commonly two), usually of unequal length 4

3′ Cell usually with two or four equal flagella; plastids two-membraned and containing chlorophyll a and b and starch as a carbohydrate storage product (Fig. 2.3 E) ..... phylum Chlorophyta

[Note: This group contains many or mostly photosynthetic members; several genera, however, have one or more species that lack chloroplasts and are thus heterotrophic, or contain chloroplasts but also exhibit heterotrophic nutrition.]

4(3) Cells without deep gullet 5

4′ Small cells with a deep, subapical gullet; two nearly equal length flagella arise from gullet (Figs. 2.3 J) ..... phylum Cryptophyta

[Note: This group contains many or mostly photosynthetic members; several genera, however, have one or more species that lack chloroplasts and are thus heterotrophic, or contain chloroplasts but also exhibit heterotrophic nutrition.]

5(4) Cells lacking the characteristics described below 6

5′ Typically with two unequal flagella; long flagellum usually directed forward during swimming, with short flagellum directed backward if emergent; compact Golgi body frequently visible anterior to nucleus of larger cells; chrysolaminarin vesicle(s) often fill posterior of cell; contractile vacuole usually present in extreme anterior end of cell; many species capable of simultaneous photosynthesis and phagocytosis (Figs. 2.2 A and 2.3 K–N) ..... phylum Chrysophyta

[Note: This group contains many or mostly photosynthetic members; several genera, however, have one or more species that lack chloroplasts and are thus heterotrophic, or contain chloroplasts but also exhibit heterotrophic nutrition.]

6(5) Without collar, or with indistinct collar 7

6′ Single anterior flagellum encircled laterally by a tentacular, funnel-shaped collar; solitary or colonial; with or without theca (Figs. 2.2 B–H) ..... class Choanoflagellida

7(6) Without protoplasmic collar 8

7′ Like Choanoflagellida above, but with second trailing flagella attached to base of lorica; protoplasmic collar; bicoecid flagellates (affinities uncertain) (Fig. 2.2 I) ..... class Bicoecea

8(7) Ventral cytostome or flagellar pocket, with associated flagella; either kinetoplast or flagellar mastigont system present; ingestion not by pseudopodia 9

8′ Flagellates with two unequal length flagella, one trailing; no kinetoplast or flagellar mastigont system; ingestion by pseudopodia (Fig. 2.2 K) ..... phylum Cercozoa

9(8) With one or usually two flagella arising from a flagellar pocket (depression); characteristically elongate or bean-shaped. Unique organelle, the kinetoplast, usually associated with the flagella (Figs. 2.2 J, L, N–P) ..... class Kinetoplastida

9′ Cells with one or two nucleus-flagella complexes (karyomastigonts) each with 1–4 flagella; no Golgi apparatus; when two karyomastigonts, mirrored symmetry of nuclei and flagella; diplomonads (Fig. 2.2 M) ..... order Diplomonadida

Protozoa: Major Groups of Amoeboid Protozoa

1 Pseudopodia either blunt and hyaline, or filiform and sometimes branching or anastomosing, or thread-like and often branching and anastomosing, or stiff and radiating 2

1′ Large, cylindrical or ovoid multinucleate amoeba; bacterial symbionts; usually containing mineral particles; nonmotile flagella-like extensions; oxygen-poor habitats (Fig. 2.5 V) ..... phylum Amoebozoa, class Archamoebea *Pelomyxa*

2(1) Pseudopodia hyaline, usually blunt, eruptive but filiform process may occur (Figs 2.4, 2.5 A–Q and 2.8 B); flagellated stages may be present 3

2′ Pseudopodia not blunt and eruptive 4

3(2) Small, usually <65 µm long, with eruptive pseudopodia, flagellated stage common in one group ..... class **Heterolobosea**, order **Schizopyrenida**

3′ No flagellated stages ..... class **Lobosea**

4(2) Pseudopodia not as filopodia 5

4′ Filiform pseudopodia (filopodia) sometimes branching or anastomosing, granular or hyaline, many with flagella at some stage in their life cycle; some with test (Figs 2.5 S–W and 2.6 A–I, K, P) ..... phylum **Cercozoa**

5(4) Pseudopodia thread-like and delicate with finely granular appearance, often branching and anastomosing to form complex reticulum (reticulopodia); test often present (Figs. 2.6 M, O, Q, R and 2.8 A) ..... traditionally grouped as phylum **Granuloreticulosea**

5′ Long, slender axopodia or filopodia radiating three-dimensionally from cell; with or without skeletal elements (Figs. 2.1 C, 2.7 and 2.8 D, I, J, L) ..... **Heliozoans** and **Pseudoheliozoans**

Protozoa: Amoeboid Protozoa: Heterolobosea: Schizopyrenida: Families

1 Amoeboid form usually cylindrical, often monopodial; usually uninucleate; nucleolus divides to form polar masses in mitosis; temporary flagellate stage common (Fig. 2.4 A, B) ..... Vahlkampfiidae

1′ Amoeba flattened or limax; often multinucleate, nucleolus disintegrates during mitosis, no flagellate stage known (Fig. 2.4 C) Gruberellidae

Protozoa: Amoeboid Protozoa: Heterolobosea: Lobosea: Families

1 Lacking external test, traditionally grouped as subclass Gymnamoebia 2

1′ Incompletely enclosed in a test or other flexible cuticle of microscales traditionally grouped as subclass Testacealobosia 10

2(1) Cylindrical or flattened; flattened forms with regular outline; no trailing uroidal filaments, with rare exceptions; not strikingly eruptive ..... order Euamoebida 3

2′ Usually flattened; frequent changes in shape typical; sometimes eruptive; subpseudopodia usually present, often furcate 8

3(2) Without subpseudopodia 4

3′ With subpseudopodia 6

4(3) Cell body flattened 5

4′ Cell body subcylindrical 7

5(4) Cell usually oblong; crescent-shaped hyaline margin at anterior end; pellicle-like layer, with dorsum often wrinkled and/or ridged; usually uninucleate; no cytoplasmic crystals (Fig. 2.4 D) ..... Thecamoebidae

5′ Body usually fan-shaped, oval, or spoon-shaped, with hyaline margin occupying up to half of length (Fig. 2.4 E) ..... Vannellidae

6(3) Subpseudopodia hyaline, blunt, digitiform, usually from anterior hyaline margin; uninucleate; nucleolar material in central body (Fig. 2.4 G) ..... Paramoebidae

6′	Few slender, conical, or linear subpseudopodia, from anterior hyaline margin or cell surface; uninucleate (Fig. 2.4 H) .... Vexilliferidae
7(4)	Most species polypodial; length usually more than 75 µm; uni- or multinucleate; numerous cytoplasmic crystals (Figs. 2.4 F, J, L)..... Amoebidae
7′	Cell monopodial, pseudopods rare; uninucleate with central nucleolus; cytoplasmic crystals in some; cysts common (Figs. 2.4 I, K)..... Hartmannellidae
8(2)	Cell flattened, triangular, trapezoid, or irregular in outline..... 9
8′	Cell regularly discoid, flattened ovoid, or fan-shaped; usually broader than wide; postcentral granular mass, usually surrounded, sometimes completely, by hyaline border with short subpseudopodia (Fig. 2.4 P)..... Hyalodiscidae
9(8)	Cell flattened, broad, and irregular in outline, though sometimes elongate during locomotion; slender tapering subpseudopodia, sometimes furcate, produced from broad, hyaline lobopodium; often with small lipid globules; uninucleate (Fig. 2.4 N)..... Acanthamoebidae
9′	Several to many fine, sometimes furcate subpseudopodia, finer than in Acanthamoebidae (Figs. 2.4 M, O) ..... Echinamoebidae
10(1)	Test more or less rigid with distinct aperture .....order Arcellinida..... 11
10′	Discoid or sometimes globose amoeba incompletely closed in a flexible tectum, no well-defined aperture (Fig. 2.5 A) ..... Cochliopodiidae
11(10)	Pseudopodia digitate and finely granular..... 12
11′	Pseudopodia conical, clear, sometimes anastomosing; test with siliceous material embedded or attached (Figs. 2.5 B, C). ..... Phryganellidae
12(11)	Test membranous or chitinoid, pliable or rigid; no plates or scales, but may have attached debris 13
12′	Test chitinoid or not, rigid, with embedded and/or attached plates, scales, siliceous granules .....suborder Difflugina..... 16
13(12)	Test round; aperture ventral .....suborder Arcellina 14
13′	Test oval to flask-shaped; nonareolar, clear; aperture terminal (Figs. 2.5 L, M) ..... Hyalospheniidae
14(13)	Test flexible to semirigid; finely or not areolate..... 15
14′	Test rigid, areolar, smooth; aperture ventral, round (Figs. 2.5 D, F, G) ..... Arcellidae
15(14)	Test not areolate; cytoplasm not enclosed in a separate membrane sac (Figs. 2.5 H, I) ..... Microcoryciidae
15′	Test finely areolate; cytoplasm enclosed in a separate membrane sac (Fig. 2.8 B)..... Microchlamyiidae
16(12)	Aperture round, broadly oval, or wavy (Figs. 2.5 J, K, N)..... Difflugiidae
16′	Aperture slit-like or narrowly oval..... 17
17(16)	Aperture terminal..... 18
17′	Aperture anteroventral, invaginated, slit-like with overhanging lip (Fig. 2.5 E)..... Plagiopyxidae
18(17)	Test particles rectangular (Figs. 2.5 O, P) ..... Paraquadrulidae
18′	Test particles not rectangular (Fig. 2.5 Q) ..... Nebelidae

Protozoa: Amoeboid Protozoa: Cercozoa: Subphyla

1	Filopodia very fine, branching or unbranching, often with obvious granules (extrusomes); many biciliate; with or without a test..... **Filosa**
1′	Filopodia or reticulopodia non-granular; cilia and test absent..... **Endomyxa**

Protozoa: Amoeboid Protozoa: Cercozoa: Filosa: Families

1	Without distinct test, sometimes with scales 2
1′	With test..... 3
2(1)	Filopodia extremely slender, branching, regularly granular; if present, cilia not visible with light microscope; cell typically small, often globular (Fig. 2.8 G)..... Limnofilidae
2′	Filopodia numerous, extremely long and branching; two long cilia sometimes present; may be found in organic mud of hot springs ..... Mesofilidae
3(1)	Test without scales; may have spines and/or attached debris 4
3′	Test with secreted, siliceous scales arranged in definitive patterns 5

4(3)	Test round, thin; may have spines or spicules (Figs. 2.5 S–U)	Chlamydophryidae
4′	Test rigid and agglutinated; cell does not fill test (Fig. 2.5 W)	Pseudodifflugiidae
5(3)	Scales not as below	6
5′	Scales round to elliptical, thin, overlapping, adjacent or scattered (Figs. 2.6 B–F)	Euglyphidae
6(5)	Scales circular or oval; test usually with aperture at end of a neck bent to one side (Figs. 2.6 G–I)	Cyphoderiidae
6′	Scales long, with long axes perpendicular to aperture; aperture at end of short neck that is not bent; test ovoid, <45 µm (Fig. 2.6 K)	Paulinellidae

Protozoa: Amoeboid Protozoa: Cercozoa: Endomyxa: Families

1	Medium to large (30 µm to >1,000 µm); filopodia nonanastomosing and more or less radiate (Fig. 2.6 A)	Vampyrellidae
1′	Small (<50 µm); filopodia lack microtubules and tend to project more from one face of the cell than from others (Figs 2.5 R and 2.6 P)	Biomyxidae

Protozoa: Amoeboid Protozoa: Granuloreticulosea

1	With a test, traditionally grouped as class Monothalamea	2
1′	Without a test, traditionally grouped as class Athalamea	3
2(1)	Test with one aperture	4
2′	Test with more than one aperture (Fig. 2.8 A)	Amphitremidae
3(1)	Test flattened on one side (Fig. 2.6 O)	Microgromiidae
3′	Test not flattened on one side (Fig. 2.6 M).	Lieberkuehnidae
4(2)	Multinucleate and highly reticulate plasmodia (Fig. 2.6 R)	Reticulomyxidae
4′	With or without anastomosing pseudopodia; one or a few nuclei; body mass more or less round (Fig. 2.6 Q)	Chlamydomyxidae

Protozoa: Amoeboid Protozoa: Heliozoa and Pseudoheliozoa

[Note: some forms with pseudopodia are members of other protist groups, for example, *Diplophrys* (Fig. 2.6L), which is a labyrinthulid.]

1	With axopodia radiating from centrosomes; axonemes visible with light microscope	2
1′	With thin, radiating filopodia; axonemes absent	pseudoheliozoans (cercozoan subphylum Filosa) 6
2(1)	Skeleton absent	3
2′	With skeleton of siliceous or organic plates and/or spicules; sometimes stalked; axopodia and stalk highly contractile (Figs. 2.7 D, F, H)	phylum Heliozoa, order Centrohelida
3(2)	With two cilia	4
3′	Cilia absent	5
4(3)	Axopodia with regularly spaced, complex extrusomes; centrosome embedded in depression of centrally located nucleus (Fig. 2.8 F)	phylum Cercozoa, family Heliomorphidae
4′	Axopodia bear moving granules; centrosome not in depression of nucleus, which is offset (Fig. 2.8 K)	Acinetactidae
5(3)	No centroplast or axoplast; axopods granule-studded and thicker at bases; large central nucleus surrounded by lacunar ectoplasm or several nuclei at periphery of central area with vesicular ectoplasm (Figs. 2.7 B, C)	order Actinophryida
5′	Microtubule organizing center of dense plaques from the nuclear membrane or from centroplast; may be confused with Actinophryida without knowledge of fine structure (origin and pattern of axopod microtubules) (Fig. 2.7 E)	order Ciliophrida
6(1)	Test with mineralized perles, or plate scales	orders Perlofilida and Rotosphaerida 7
6′	Cell enclosed by a latticed organic capsule (skeleton), a rigid theca, or by irregular particles adhering to the outer surface	12
7(6)	Test of mineralized spherical perles; outer layer with apically pointed silica scales (Fig. 2.8 J)	order Perlofilida, Acanthoperlidae
7′	Test of plate scales	order Rotospherida and Perlofilid family Pompholyxophryidae 8
8(7)	Test typically with two-tier plate scales; flagella absent	order Rotospherida 9
8′	Body spherical, coated with a single layer of siliceous perles (Fig. 2.8 L)	Pompholyxophryidae
9(8)	Test with columnar radial spines, flared out both basally and apically	10

9′	Test without columnar spines	11
10(9)	Outer plate scales with single, large hole (Fig. 2.8 D)	Rabdiophryidae
10′	Outer plate scales without holes (Fig.2.8 E)	Rabdiasteridae
11(9)	With scalloped test of regular, unperforated cup-shaped scales; filopodia in groups of 1−3 (Fig 2.8 H)	Cathrellidae
11′	Test not scalloped; filopodia extremely thin, not in groups (Fig 2.8 C)	Piaciophoridae
12(6)	Cell enclosed in latticed organic capsule (skeleton); generally stalked; no centroplast; cell body spherical in adults (Fig. 2.7 A)	order Desmothoracida
12′	Cell enclosed in rigid theca with many tine pores through which filopodia emerge; filopodia with long, thin extrusomes (Fig. 2.7 G)	subclass Testosia, Lithocollidae

Protozoa: Ciliophora: Classes and Subclasses

1	Cilia present in trophont (active) stages; retractile suctorial tentacles only in family Actinobolinidae (class Litostomatea, order Haptorida)	2
1′	Suctorial tentacles present (absent in one endocommensal group); no true cytostome or cytopharynx; adults (trophonts) usually sessile, many species ectosymbiotic, some planktonic species; cilia absent except in free-swimming dispersal larval stages; with or without lorica	class Phyllopharyngea, subclass **Suctoria**
	[Note: Patterns of division and release of the larvae form the basis for dividing the subclass into orders. Other characters are useful in identification, but knowledge of the full life cycle is often required before suctorians can be confidently assigned to a genus.]	
2(1)	Conspicuous buccal ciliature at apical pole; buccal ciliature winds clockwise toward the center when viewed from oral end; somatic ciliature reduced or absent; mobile or sessile; solitary, gregarious or colonial; some species loricate; oral region can contract and withdraw in most species; with either scopula or complex adhesive disc (holdfast) at aboral end of cell	class Oligohymenophorea ... subclass **Peritrichia** 3
2′	Not as above: without scopula or complex adhesive disc at aboral end of cell	4
3(2)	Trophont mobile; symbiotic on other organisms; with complex adhesive disc (holdfast) at aboral end of cell	order **Mobilia**
3′	Trophont only rarely motile, usually attached to substratum, which may be inanimate objects or other organisms, via a stalk, lorica or scopula; many gregarious or colonial species	order **Sessilida**
4(2)	Oral area not bordered by an adoral zone of membranelles; no ventral cirri	5
4′	Oral area usually bordered by a well-developed adoral zone of membranelles (AZM) consisting of more than three membranelles (polykineties); with or without ventral cirri.	11
5(4)	Cytostome at end of a buccal cavity or vestibulum with cilia or paroral membrane(s) associated	6
5′	Cytostome at or near surface; buccal cavity, if present, without cilia or paroral membranes	7
6(5)	Alveoli well developed and revealed as a prominent argyrome, typically reticulate; body shape variable, many reniform and flattened	class **Colpodea**
6′	Alveoli not well developed, no prominent argyrome; body typically ovoid to elongate ovoid elongate ovoid	class **Oligohymenophorea**
7(5)	Cytostome lateral or ventral	8
7′	Cytostome at or near anterior end, or continuing down side as a slit	9
8(7)	Circular mouth located midventrally; no proboscis; large cytostome	10
8′	Cytostome a barely visible lateral slit on the convex side of a tapering front end, or a lateral opening at the base of an anterior proboscis (Fig. 2.9 J); see also Spathidiidae (Figs. 2.10 I, U)	class Karyorelictea, Loxodidae
9(7)	Oral ciliature as simple kinetids; with dorsal brosse or brush formed of specialized dikinetids bearing clavate cilia	class **Litostomatea**
9′	With circumoral ciliation composed of dikinetids; without dorsal brosse	class **Prostomatea**
10(8)	Body nearly ellipsoid, rounded in cross-section, sometimes flattened ventrally; medium to large (some 100 μm); densely ciliated all over; oral depression present	class **Nassophorea**
10′	Body usually flattened; ventrum ciliated, dorsum bare or with a few cilia; anterior preoral arcs of right ventral ciliary rows continuous with more posterior parts	class Phyllopharyngea, subclass **Cyrtophoria**
11(4)	Somatic ventral ciliature as polykinetids (cirri) in groups or files on ventral surface	12
11′	Somatic ciliature as monokinetids or dikinetids, but not cirri	14
12(11)	Body typically oval to rectangular, sometime ellipsoidal, rigid and dorsoventrally flattened, often heavily ribbed; ventral cirri often conspicuous; pellicular alveoli well developed	13
12′	Body elongate, often flexible; ventral cirri often inconspicuous; pellicular alveoli poorly developed;	class Spirotrichea, subclass **Stichotrichia**

13(12) Body ovoid with prominent longitudinal ridges on each side; AZM stretching almost entire body length terminating near posterior pole; ventral ciliature comprising delicate cirri in widely spaced rows (Fig. 2.18 E) ..... class Spirotrichea, subclass Protocruziidia, Phacodiniidae

13′ Body ovoid to rectangular or ellipsoidal; AZM not usually stretching to posterior pole ..... .class Spirotrichea, subclass **Hypotrichia**

14(11) Somatic cilia sparse or absent 15

14′ Body surface densely ciliated 16

15(14) Body flattened, rigid, often with spines; body ciliature present as short, generally obvious rows; oral ciliature relatively inconspicuous; mainly anaerobic ..... class **Plagiopylea**

15′ Membranelles numerous in complete, or almost complete, circle at oral end; body generally conical or bell-shaped; mostly planktonic ..... class Spirotrichea, subclasses **Choreotrichia** and **Oligotrichia**

16(14) Body small to medium, usually twisted to left; oral region spiraled with paramembranelles; with hydrogenosomes instead of mitochondria; in richly organic sediments with low, or no, oxygen ..... class **Armophorea**

16′ Body medium to large, often elongate and contractile; somatic ciliation holotrichous; left oral polykinetids conspicuous, typically paramembranelles encircling the anterior end clockwise before plunging into the oral cavity; one or more parorals on right side ..... class **Heterotrichea**

Protozoa: Ciliophora: Suctoria: Orders

1 Budding begins in a pouch 2

1′ Budding and cytokinesis on surface of trophont ..... **Exogenida**

2(1) Exogenous budding occurring in a brood pouch; swarmers become free-swimming in pouch before emerging through birth pore; swarmer small and ciliated ..... **Endogenida**

2′ Cytokinesis of swarmer completed exogenously, after the emergence of everted bud on cell surface; swarmer often ellipsoidal, flattened ..... **Evaginogenida**

Protozoa: Ciliophora: Suctoria: Exogenida: Families

1 Trophont sac-like or spherical, basally attached to bottom of lorica near junction with stalk 2

1′ Trophont not sac-like, not basally attached to lorica, or without lorica 3

2(1) Tentacles capitate, grouped apically in single fascicle or row; swarmers ovoid with somatic kineties around body (Fig. 2.13 B) ..... Paracinetidae

2′ Tentacles clavate, in a group on narrow, rounded distal end of body; swarmers flattened or vermiform, ciliated on one margin (Fig. 2.14 A) ..... Thecacnetidae

3(1) Without a rod-like tentacle or protuberance of stylotheca 4

3′ Ectoparasitic, attached to host (usually peritrich ciliates) by rod-like tentacle or protuberance of stylotheca (Fig. 2.16 L) ..... Manuelophryidae

4(3) Trophont medium to large, cylindrical, conical, or trumpet-shaped; ectocommensal on crustaceans (Fig. 2.18 B) ..... Spelaeophryidae

4′ Trophont small to medium, spheroid, pyriform, or goblet-shaped 5

5(4) Lorica with several radial slits in distal half through which tentacles project; sometimes stalked; free-living or ectocommensal on invertebrates or other ciliates (Fig.2.13 C) ..... Metacinetidae

5′ Typically aloricate and stalked 6

6(5) Trophont goblet-shaped or laterally flattened; attached to antennules of harpacticoid copepods (Fig. 2.13 L) ..... Lecanophryidae

6′ Trophont spheroid or pyriform; planktonic or sessile, often attached to other ciliates as parasites (Figs. 2.14 E, G) ..... Podophryidae

Protozoa: Ciliophora: Suctoria: Endogenida: Families

1 With stalk 2

1′ Without stalk 5

2(1) With lorica 3

2′ Without lorica 4

3(2)	Trophonts laterally flattened, trapezoid, triangular, or discoid; lorica often triangular; one type of tentacle arranged in two, rarely three, fascicles or rows (Fig.2.14 F)..... Acinetidae
3′	Trophont trapezoid, laterally flattened; loricate; tentacles of two types, i.e., agile prehensile and regular feeding ones; ectosymbionts on plants and invertebrates (Fig. 2.16 B)..... Acinetopsidae
4(2)	Trophont globular to ellipsoidal; tentacles funnel-like; attached to cyclopoid crustaceans (Fig. 2.13 D) ..... Choanophryidae
4′	Trophont ovoid, cylindrical, or triangular, often flattened; tentacles capitate; free-living (Figs. 2.14 K, L) ..... Tokophryidae
5(1)	Without lorica or, if present, lorica mucoid..... 6
5′	Trophont small, spheroid to ovoid; tentacles capitate; with lorica that is attached to substrate by basal surface; in periphyton or plankton (Fig. 2.13 E) ..... Solenophryidae
6(5)	Tentacles present..... 7
6′	Tentacles absent; trophont ovoid to spheroid; endoparasitic in cells and tissues of hosts such as other ciliates and invertebrates (Fig. 2.13 I) ..... Endosphaeridae
7(6)	Attached to substratum by basal body surface or protuberance of body..... 8
7′	Attached to substratum by tentacles or cinctum..... 10
8(7)	Trophont ovoid, pyriform, truncate or branching..... 9
8′	Trophont flattened; some species in mucoid lorica; tentacles capitate or rod like; ectocommensals on invertebrates and vertebrates including the gills of fishes (Fig. 2.18 K)..... Trichophryidae
9(8)	Trophont small, pyriform to ovoid; tentacles agile, very flexible; ectoparasites on crustaceans (Fig. 2.18 J) ..... Rhynchetidae
9′	Trophont medium to large, pyriform to truncate to branching; tentacles capitate not conspicuously flexible; some free-living, some endosymbionts some ectosymbionts on turtles or the gills of crustaceans (Fig. 2.15 A)..... Dendrosomatidae
10(7)	Trophonts small to medium, ovoid to irregular; attached to host by arm-like cinctum; hypocommensals on peritrich ectosymbionts of fishes (Fig. 2.18 C) ..... Erastophryidae
10′	Trophonts small, globular to ellipsoid; with lorica; tentacles rod-like, one to several serving both for feeding and attachment; parasites of other ciliates (e.g., folliculinids and suctorians) (Fig. 2.16 J) ..... Pseudogemmidae

Protozoa: Ciliophora: Suctoria: Evaginogenida: Families

1	Tentacles present; not parasites of rotifers..... 2
1′	Tentacles absent; trophont small and sac-like; stalk absent; swarmer ellipsoidal, flattened, with several longitudinal kineties; parasites of tissues of rotifers (Fig. 2.16 K) ..... Trypanococcidae
2(1)	Tentacles ramified..... 3
2′	Tentacles not ramified 4
3(2)	Trophont vase-like, branched, lifted off substrate by basal protuberance; ectocommensals on gammarid crustaceans (Fig. 2.18 D) ..... Cometodendridae
3′	Trophont hemispherical or disc-shaped, unbranched, basal protuberance absent; ectocommensals on gammarid amphipods (Figs. 2.14 I, O) ..... Dendrocometidae
4(2)	Tentacles capitate..... 5
4′	Tentacles not capitate 6
5(4)	Trophont small, spheroid; stalked; tentacles evenly distributed over body; macronucleus globular; in periphyton (Fig. 2.13 F) ..... Prodiscophryidae
5′	Trophont small to medium, discoid, sometimes sac-like; sometimes stalked; tentacles in fascicles or evenly distributed over body; macronucleus ellipsoid, ribbon-like or ramified; in periphyton or ectocommensal on arthropods (Figs. 2.14 M, N)..... Discophryidae
6(4)	Tentacles rod like, neither solitary nor in fascicles..... 7
6′	Tentacles clavate or knobbed, either solitary or in fascicles..... 8
7(6)	Trophont small, ovoid to spheroid; without stalk or lorica; tentacles on one side of body only; macronucleus globular; hydrogenosomes present; in anaerobic or microaerophilic habitats (Fig. 2.16 C) .....Enchelyomorphidae
7′	Trophont small to medium, ovoid, discoid or sac-like, spread over substratum; sometimes stalked; tentacles rod-like, evenly distributed or arranged in rows; macronucleus elongate ellipsoid; ectocommensal on isopod and amphipod crustaceans (Fig. 2.18 L) ..... Stylocometidae
8(6)	Stalk absent..... 9

8′ Stalk present; trophont small, elongate, laterally flattened; tentacles agile and contractile; macronucleus ribbon-like; ectoparasites of discophryid suctorians (Fig. 2.15 B) ..... Rhynchophryidae

9(8) Trophonts discoid, often flattened, attached to substratum by adhesive disc; lorica absent; tentacles knobbed, extensible, solitary or in fascicle; in periphyton or ectocommensal on invertebrates (Fig. 2.14 J) ..... Heliophryidae

9′ Trophont laterally flattened; with lorica or stylotheca; tentacles clavate, in fascicles; in periphyton or endocommensal on invertebrates (Fig. 2.15 C) ..... Periacinetidae

Protozoa: Ciliophora: Oligohymenophorea: Peritrichia: Mobilida: Families

1 Denticles of holdfast with hooks and spines; ectosymbionts on a wide range of vertebrate and invertebrates hosts, e.g., *Hydra*, fishes, amphibians (Fig. 2.12 D)..... Trichodinidae

1′ Denticles of holdfast simple, toothed; elongated macronucleus, ectosymbionts on turbellarians (Fig. 2.12 C); ..... Urceolariidae

Protozoa: Ciliophora: Oligohymenophorea: Peritrichia: Sessilida: Families

1 Attached to substratum via a stalk, lorica, or scopula; one genus (*Planeticovorticella*) unattached..... 2

1′ Free-swimming, without stalk or lorica; swims with oral end forward; with or without aboral ring of cilia (Figs. 2.12 A, B) .... Astylozoidae

2(1) Stalked or, if stalkless, with lorica..... 3

2′ Without stalk or lorica, attached to substratum via scopula; solitary; epibionts of invertebrates or on the gills of fishes (Fig. 2.12 E) .... Scyphidiidae

3(2) With contractile stalk, although *Ophrydium* has a noncontractile stalk (Fig. 2.12 J); solitary or colonial 4

3′ If stalked, stalk noncontractile; solitary or colonial 5

4(3) Stalk contracts in a spiral fashion; in colonial forms, stalk myoneme discontinuous so each zooid or branch contracts independently (Figs. 2.12 K, Q, R)..... Vorticellidae

4′ Stalk contracts in a zig-zag or other fashion, but not spirally; in colonial forms stalk myoneme continuous so colony contracts in union (Figs. 2.12 H, I) ..... Zoothamniidae

5(3) With lorica 6

5′ Without lorica (although lorica may be present in some species; if in doubt follow both parts of key) 9

6(5) Lorica ovoid or hemispheroid, flattened; if present, peristomial lip rigid 7

6′ Lorica conical to cylindrical, generally slender; peristomial lip retractable 8

7(6) Lorica aperture closeable by lip-like folds; peristomial lip absent; symbionts of invertebrates or attached to aquatic plants (Fig. 2.15 L) ..... Lagenophryidae

7′ Lorica aperture not closeable; peristomial lip present; attached to isopod crustaceans (Fig. 2.13 H) ..... Usconophryidae

8(6) Stalk in two parts, a contractile proximal part within the lorica, and a noncontractile distal part outside the lorica; attached to crustaceans (Fig. 2.18 I)..... Rovinjellidae

8′ If present, stalk noncontractile; lorica generally slender; zooid typically extends well beyond opening of lorica; attached to plants, inanimate objects or as symphorionts (Figs. 2.12 F, G, L–N). ..... Vaginicolidae

9(5) Peristomial disc raised on a short neck; peristomial lip absent; some species with a highly developed theca; stalked; commonly as epibionts of arthropods but also on inanimate objects (Fig. 2.12 S) ..... Opercularidae

9′ Peristomial disc not raised on a short neck; peristomial lip present; stalked; solitary or colonial; symphorionts on a wide range of hosts, or on inanimate objects (Figs. 2.12 O, P, T, U) ..... Epistylididae

Protozoa: Ciliophora: Colpodea: Families

1 Body ovoid; oral region large relative to body size; argyrome "kreyellid," i.e., highly reticulated and densely subdivided 2

1′ Body shape variable; argyrome "colpodid" or "playophorid," i.e., not highly reticulated or densely subdivided..... 3

2(1) Body length exceeds 40–50 µm; somatic ciliation holotrichous forming a conspicuous postoral suture (Fig. 2.13 G) .... Bryometopidae

2' Body flattened, length less than 40–50 µm; somatic ciliation reduced or absent on dorsal and left sides (Fig. 2.16 G) ..... Kreyellidae

3(1) Body asymmetric, often reniform or ovoid with lobes; paroral as few to many rows, often disordered 4

3′	Body elongate ovoid or reniform; paroral as a single row of dikinetids 6
4(3)	Oral region not conspicuously large relative to body size; aperture opening round to reniform; vestibulum funnel-shaped, extends from ventral to dorsal side 5
4′	Oral apparatus very large; oral opening conspicuously key hole-shaped, occupies anterior area and extends to mid-region of cell; body large to very large (Fig. 2.10 C) ..... Bursariidae
5(4)	Body typically reniform; oral apparatus in anterior half of body; division in a cyst (Figs. 2.17 N, P–S) ..... Colpodidae
5′	Body ovoid with large preoral and small postoral lobes; oral apparatus in posterior half of body; often enclosed in gelatinous lorica but some species only rarely build, or readily desert, the lorica (Figs. 2.17 K,L) ..... Marynidae
6(3)	Body broad-to-narrow ovoid; oral region equatorial to apical; paroral as a file of kineties on right, few to many polykineties on left; micronucleus in perinuclear space of macronucleus 7
6′	Body elongate ovoid; oral opening distinctly subapical, shallow or funnel-shaped; micro- and macronuclei with separate nuclear membranes; typically found in temporary ponds (Fig. 2.15 K) ..... Bryophryidae
7(6)	Body small to large; oral region in anterior one-third of body; somatic ciliation holotrichous 8
7′	Body small, ovoid; oral region equatorial, with distinct cytopharyngeal basket; somatic kineties only on right (=ventral) surface (Fig.2.16 I) ..... Pseudochlamydonellidae
8(7)	Body broad or elongate ovoid, never in a lorica; paroral not segmented; several to many left polykinetids 9
8′	Body narrow ovoid, sometimes in a gelatinous lorica; paroral in two segments, anterior of which is conspicuously ciliated, posterior inconspicuous; 3–5 left polykinetids (Fig. 2.9 K) ..... Cyrtolophosididae
9(8)	Body broadly ovoid; oral region subapical on right side, slanted, with distinctive adoral zone that is longer than the paroral (Fig. 2.16 M) ..... Woodruffiidae
9′	Body elongate ovoid; oral region near truncated anterior margin; length of adoral zone about equal to paroral (Fig. 2.18 G) ..... Platyophryidae

Protozoa: Ciliophora: Oligohymenophorea: Subclasses

[Note: identification of these subclasses and the taxa within them is difficult without special preparation techniques, such as silver staining.]

1	Somatic kinetids mostly as dikinetids; postoral suture may be present 2
1′	Somatic kinetids as monokinetids; with preoral suture but no postoral suture; mouth in anterior quarter of cell ..... **Hymenostomatia**
2(1)	Somatic ciliation typically dense with preoral and postoral sutures; oral polykinetids typically elongate and parallel to long axis of oral cavity; extrusomes mostly as trichocysts; scutica absent ..... **Peniculia**
2′	Somatic ciliation sometimes sparse; oral region variable in shape; extrusomes mostly as mucocysts; scutica present ..... **Scuticociliatia**

Protozoa: Ciliophora: Hymenostomatia: Families

1	Body small to large, elongate ovoid to spherical; somatic ciliation very dense; histophagous on invertebrates or parasites of fishes; with organelle of Lieberkühn (watchglass organelle) 2
1′	Body usually small to medium, sometimes large, ovoid or pyriform; primarily bacterivorous but some histophagous or parasitic; without organelle of Lieberkühn 3
2(1)	Theront elongate ovoid, tomont spherical; caudal cilium present in theront; parasitic invading the gills and integuments of fishes causing white spot disease (Fig. 2.15 I) ..... Ichthyophthiriidae
2′	Elongate ovoid; posterior end of polykinetid 2 enlarged and beats like a brush; histophagous on invertebrates or parasitic on mollusks (Fig. 2.15 H) ..... Ophryoglenidae
3(1)	Body ovoid, ellipsoid, cylindrical or pyriform; right ventral kineties do not twist abruptly to run parallel to anterior suture (except in *Glaucomella*) 4
3′	Body elongate ovoid, sometimes tapering posteriorly; right ventral kineties curving left, twisting abruptly anterior of the oral region, to run parallel to the anterior suture (Figs. 2.17 F, H) ..... Turaniellidae
4(3)	Body pyriform to cylindrical; bases of membranelles of uniform width; paroral ciliated along its entire length; mouth roughly triangular; most species free-living but some as facultative or obligate parasites in a wide range of hosts (Figs. 2.1 D and 2.17 O) ..... Tetrahymenidae
4′	Body ovoid to ellipsoid; oral cavity relatively large; posterior portion of paroral unciliated; with two conspicuous oral membranelle-like "lips" that seem to vibrate; free-living, sometimes carnivorous (Fig. 2.17 C) ..... Glaucomidae

Protozoa: Ciliophora: Peniculia: Families

1 Oral region conspicuously large, covering most of ventral surface 2

1′ Oral region typically covers <50% of ventral surface 3

2(1) Body distinctly cordate or conical with flattened ventral surface and humped dorsal surface; mouth V-shaped; left oral cilia as widely spaced polykinetids (Fig. 2.17 B) ..... Stokesiidae

2′ Body broadly ovoid; cilia of paroral membrane long, left oral cilia appearing as one long polykinetid (Fig. 2.17 G) ..... Lembadionidae

3(1) Body ovoid or elongate ovoid; somatic ciliation holotrichous 4

3′ Body short, cylindrical, with larger rounded anterior half; somatic ciliation as a distinct equatorial girdle; caudal cilia forming a conspicuous tuft used for temporary attachment (Fig. 2.17 D) ..... Urocentridae

4(3) Mouth area sunken in, with oral groove leading to it, or with ciliated pharyngeal tube, or both 5

4′ Mouth area subapical and elongate; prebuccal area shallow or absent; usually with many ophrokineties to right of buccal region; nematodesmata prominent to side and rear of mouth; contractile vacuoles with long collecting canals (Figs. 2.17 A, E) ..... Frontoniidae

5(4) Mouth within an oral vestibule; nematodesmata form a ring or "basket" around mouth (Fig. 2.17 J) ..... Clathrostomatidae

5′ Medium to large (150 µm in some species); body foot-shaped or ellipsoidal, with pointed or rounded caudal end; long, broad, ciliated oral groove leads into buccal cavity; two contractile vacuoles; one species with algal symbionts (Fig. 2.17 I) ..... Parameciidae

Protozoa: Ciliophora: Scuticociliatia: Families

1 With linear oral furrow or groove leading from anterior end to mouth bordered on right by paroral membrane 2

1′ Without linear preoral groove bordered by membranes, but generally with membranes inside oral cavity 7

2(1) Paroral membrane along furrow *not* double 3

2′ With an apparent double paroral membrane on the right side of the furrow (actually the paroral membrane plus a row of somatic cilia) (Fig. 2.9 T) ..... Cohnilembidae

3(2) Bottom of preoral furrow not ciliated, paroral membrane curves around rear of mouth 4

3′ Preoral furrow long, shallow, ciliated with three ciliary fields; generally a single caudal cilium; body long, ovoid (Figs. 2.9 L–N) ..... Philasteridae

4(3) Does not produce a lorica 5

4′ Dwells in lorica that is open at both ends; resembles *Pleuronema* or *Cyclidium* (Fig. 2.9 X) ..... Calyptotrichidae

5(4) Medium to large; somatic ciliation often dense; long, stiff cilia present either caudally or interspersed between regular cilia 6

5′ Very small to small (15–60 µm long); somatic ciliation sparse; single, conspicuous distinct caudal cilium (Fig. 2.9 W) ..... Cyclidiidae

6(5) Paroral membrane a prominent velum extending from anterior to well past equator of cell; one to many stiff, long caudal cilia (Fig. 2.9 R) ..... Pleuronematidae

6′ Somatic ciliation dense with long, stiff, bristle-like cilia interspersed between regular cilia over body surface; paroral membrane less prominent than above (Fig. 2.9 S) ..... Histiobalantiidae

7(1) With 1–2 girdles of cilia 8

7′ Cilia not in girdles, usually in longitudinal rows 9

8(7) Oral cavity equatorial; distinct constriction in the ciliated girdle; ends bare except for caudal cilium (Fig. 2.9 P) ..... Urozonidae

8′ Oral cavity deep, equatorial; two distinct ciliary girdles; ciliary tuft on posterior end (Fig. 2.17 D) ..... Urocentridae

9(7) Mouth at, or anterior to, middle of cell 10

9′ Oral area large, toward posterior half of cell (midventral); body usually flattened; cilia denser ventrally (Fig. 2.9 V) ..... Cinetochilidae

10(9) Small, <50 µm; anterior pole flat, unciliated (Fig. 2.9 U) ..... Uronematidae

10′ Somatic ciliation even; body long-ovoid; oral area small, closer to anterior end (Figs. 2.9 O, Q) ..... Loxocephalidae

Protozoa: Ciliophora: Litostomatea: Orders

1	Oral region typically circular surrounded by circumoral dikinetids 2
1′	Oral region elongated with slit-like cytostome and oral kinetids as left and right components that extend along the edge of the laterally flattened body; somatic ciliation on both sides of body, typically more dense on the right side ..... **Pleurostomatida**
2(1)	Oral region apical and domed, without nematodesmata or microtubules of rhabdos; somatic cilia bristle-like, of at least two types, arranged in girdles around the body; body globular to subspheroid..... .order Cyclotrichiida (Figs. 2.10 L, N) ..... Mesodiniidae
2′	Oral region with microtubules or nematodesmata of rhabdos; somatic ciliation holotrichous, but restricted to girdles in didiniids .... **Haptorida**

Protozoa: Ciliophora: Litostomatea: Pleurostomatida: Families

1	Right somatic kineties converge forming a spica in anterior midregion; oral region with one left and one right perioral kineties (Fig. 2.9 F) ..... Amphileptidae
1′	Right somatic kineties terminate along rightmost perioral kinety, thus spica absent; oral region with one left and two right perioral kineties (Figs. 2.9 G, I) ..... Litonotidae

Protozoa: Ciliophora: Litostomatea: Haptorida: Families

1	Somatic cilia not arranged in girdles around body..... 2
1′	Somatic cilia arranged in one or two girdles that encircle the body (Figs. 2.10 V, W)..... Didiniidae
2(1)	Apex fan-shaped to varying degrees; mouth a long slit, beginning at anterior end; slit may extend down side of cell, or at lasso-shaped oral bulge..... 3
2′	Mouth at anterior end, rounded or only slightly elongated..... 4
3(2)	Body flattened with obliquely truncate anterior end; oral region usually elongate dorsoventrally with slit-like cytostome; circumoral dikinetids as proliferated anterior fragments of somatic kineties (Figs. 2.10 I, U)..... Spathidiidae
3′	Body elongate ovoid; oral region apical or subapical forming a lasso-shaped bulge surrounded by an unclosed ring of circumoral dikinetids (Fig. 2.13 J)..... Apertospathulidae
4(2)	Without tentacles 5
4′	Body ovoid; with tentacles extending from the cell in all directions when at rest, but retracted and hardly visible when swimming (Fig. 2.10 G) ..... Actinobolinidae
5(4)	Anterior tapering to a ciliated neck; neck set off by groove and a circle of longer cilia; contractile (Fig. 2.10 K) ..... Lacrymariidae
5′	Not as above 6
6(5)	Oral region apical; body lacks a dorsal proboscis..... 7
6′	Oral region distant from apical region and lies at base of dorsal proboscis.....(Figs. 2.9 D, E, H)..... Tracheliidae
7(6)	Oral region apical but not forming a dome 8
7′	Oral region simple dome, sometimes pointed 9
8(7)	Body ovoid to fusiform, usually shorter than four times width; oral region flat, often at end of extensible neck; 2–4 brosse knieties (Figs. 2.10 Q–S) ..... Enchelyidae
8′	Body small, ovoid to elongate; without an extensible neck; brosse kineties of many rows in which clavate dikinetids alternate with typical somatic monokinetids (Fig. 2.18 M)..... Pseudoholophryidae
9(7)	Long-ovoid or flask-shaped; oral region circular to elliptical; circumoral dikinetids at end of, and never exceeding the number of, somatic kineties (Fig. 2.10 P) ..... Trachelophyllidae
9′	Ovoid to elongate; oral region apical with oral dikinetids evenly surrounding cytostome; somatic ciliation often more dense in anterior half (Fig. 2.10T)..... Acropisthiidae

Protozoa: Ciliophora: Prostomatea: Orders

1 Body ovoid to cylindroid; somatic ciliation holotrichous, sometimes reduced in posterior half and lacks obvious radial symmetry; brosse present; toxicysts present in oral region ..... **Prorodontida**

1′ Body cylindroid; somatic ciliation holotrichous with clear radial symmetry; brosse and toxicysts absent ..... **Prostomatida**

Protozoa: Ciliophora: Prostomatea: Prorodontida: Families

1 Body without armour plates 2

1′ Translucent $CaCO_3$ plates (armour) in cortex; typically cylindrical; body frequently spiny, often with prominent anterior and caudal thorns; long caudal cilium common; brosse present, but inconspicuous (Fig. 2.10 H) ..... Colepidae

2(1) Posterior region of body ciliated 3

2′ Posterior one-third to one-fifth of body unciliated, except for one or more long caudal cilia; other somatic ciliation evenly distributed (Fig. 2.10 M) ..... Urotrichidae

3(2) Brosse inconspicuous, comprising 3 or 4 units either between perioral and circumoral ciliature, or on posterior right of oral area; body small, ovoid or pyriform 4

3′ Brosse as an extension of the unclosed circumoral ciliature or as several to many kinetofragments 5

4(3) Body pyriform; somatic ciliation as a girdle encircling cell apex; brosse as 3 or 4 inconspicuous rows between perioral and circumoral ciliature (Fig. 2.18 H) ..... Lagynidae

4′ Body ovoid; somatic ciliation holotrichous; oral region with extensible lappets; brosse as 3 units on posterior right of oral area (Fig. 2.16 E) Plagiocampidae

5(3) Brosse short, extending backward from apical mouth on one side; body ellipsoid (Figs. 2.9 A, B) ..... Prorodontidae

5′ Brosse as several to many kinetofragments; body ovoid to cylindroid; oral region apical to subapical, surrounded by circumoral dikinetids; similar to and easily confused with *Prorodon* (Fig. 2.9 C) ..... Holophryidae

Protozoa: Ciliophora: Prostomatea: Prostomatida: Families

1 Free-swimming but living in a pseudochitinous lorica; one or more caudal cilia; pantenes conspicuous (Figs. 2.10 J, O) ... Metacystidae

1′ Without a lorica; pantenes present but not conspicuous; somatic kineties mostly bipolar, oral region apical, surrounded by simple dikinetids (Fig. 2.13 K) ..... Apsiktratidae

Protozoa: Ciliophora: Nassophorea: Families

1 Somatic ciliature relatively sparse with few, widely separated kineties, kinetosomes without proximal and distal cartwheel; cyrtos small; somatic extrusomes as trichocysts ..... order Microthoracida 2

1′ Somatic ciliature usually dense with closely spaced kineties, kinetosomes with proximal and distal cartwheel; cyrtos large; frange with polykinetid extending left from postoral region, sometimes to dorsal surface ..... order Nassulida (Fig. 2.12 Z), Nassulidae

2(1) Cytostome in rear half of body; small cyrtos hidden by ventral pellicular fold (Fig. 2.12 W) ..... Microthoracidae

2′ Cytostome opens laterally in anterior third of body, long tubular cyrtos; body nearly oval (Fig. 2.12 V) ..... Leptopharyngidae

Protozoa: Ciliophora: Phyllopharyngea: Families

1 Dorsal and ventral surfaces join with a simple margin, without a "railway track-like" groove 2

1′ Dorsal and ventral surfaces separated by a "railway track-like" groove; typically >3 oral kineties (Fig. 2.16 A) ..... Lynchellidae

2(1) Body ovoid and flattened; oral opening as large transverse groove; oral ciliature as a single kinety encircling oral opening (Fig. 2.13 A) ..... Gastronautidae

2′ Body width two-thirds length, with prominent beak-like protuberance in anterior left; oral ciliature as one preoral and two circumoral kineties (Fig. 2.17 T) ..... Chilodonellidae

Protozoa: Ciliophora: Spirochotrichea: Stichotrichia: Orders

1	Ventral cirri arranged in longitudinal files, either linear or zig-zag 2
1′	Ventral cirri heavy and conspicuous, typically arranged in localized groups; body outline often oval to elliptical, sometimes elongate .... **Sporadotrichida**
2(1)	Frontoventral cirri arranged in longitudinal or zigzag files ..... **Urostylida**
2′	Frontoventral cirri arranged in one or more linear files (not zigzag); body outline typically elongate, sometimes very drawn out posteriorly ..... **Stichotrichida**

Protozoa: Ciliophora: Spirotrichea: Stichotrichia: Sporadotrichida: Families

1	Small to large, elongate, sometimes tailed; two or more macronuclear nodules 2
1′	Small, spheroid to subovoid; somatic ciliature reduced to a few long (>10 μm, often stiff) bristle-like cirri arranged circumferentially around the equator effecting a jumping motion; single macronucleus (Fig. 2.11 W) ..... Halteriidae
2(1)	Ventral cirri in anterior and posterior regions but not in midbody; two to many macronuclear nodules (Fig. 2.13 N) ... Trachelostylidae
3′	Ventral cirri large and distinctive, typically 18 in number, scattered over body including midbody; typically two macronuclear nodules (Figs. 2.11 A, C, E) ..... Oxytrichidae

Protozoa: Ciliophora: Spirotrichea: Stichotrichia: Urostylida: Families

1	Midventral complex with a single zigzag file of paired cirri and with or without marginal rows 2
1′	Body medium to large, elongate ovoid; frontoventral cirral zigzag with 1−6 files; multiple left and right marginal cirral rows (Fig. 2.15 E) Pseudourostylidae
2(1)	Frontal cirri in a bicorona; midventral complex comprises midventral cirral pairs only; one marginal row on each side; caudal cirri absent (Fig. 2.15 J) ..... Pseudokeronopsidae
2′	Many frontal cirri arranged in a bicorona, tricorona, or multicorona; midventral complex often with midventral rows; often >1 marginal row on each side; caudal cirri often present (Figs. 2.11 B, D) ..... Urostylidae

Protozoa: Ciliophora: Spirotrichea: Stichotrichia: Stichotrichida: Families

1	Two or more ventral cirral files; when present, marginal rows often not extending entire body length 2
1′	Ventral cirri in a single file; marginal rows typically extending entire body length (Fig. 2.18 F) ..... Amphisiellidae
2(1)	Ventral files not ending on dorsal surface; dorsal files not winding helically around body 3
2′	Ventral cirral files curved or spiraling around body, some ending on dorsal surface; dorsal files in a strip that winds helically around body (Fig. 2.15 F) ..... Spirofilidae
3(2)	Transverse and caudal cirri present 4
3′	Transverse and caudal cirri absent; medium to large, elongate ovoid; typically >2 midventral files (Fig. 2.13 O) ..... Kahliellidae
4(3)	Ventral cirral files in several oblique rows, first row curved along anterior border; ventral cirri generally in several oblique rows between right and left marginal rows (Fig. 2.15 G) ..... Keronidae
4′	Ventral cirri long and sparse; marginal cirri strongly reduced; oval to elliptical, sometimes with spiny posterior extensions and/or zoochlorellae (Fig. 2.16 D) ..... Psilotrichidae

Protozoa: Ciliophora: Spirotrichea: Hypotrichia: Families

1	Body dorsoventrally flattened, sometimes ridged; ventral ciliation as cirri arranged in localized groups 2
1′	Body ellipsoidal; somatic ciliation as delicate cirri in files; oral cavity supported by a basket of nematodesmata (Fig. 2.15 D) ..... Reichenowellidae
2(1)	AZM reduced, located centrally and inconspicuous; no left marginal or caudal cirri; transverse cirri conspicuous (Fig. 2.12 X) Aspidiscidae
2′	AZM well developed and conspicuous in anterior half of body; marginal and caudal cirri present (Fig. 2.12 Y) ..... Euplotidae

Protozoa: Ciliophora: Plagiopylea: Families

1 Body round to discoidal, helmet-shaped or box-shaped, laterally compressed, with armour-like cuirass and often short spines 2

1′ Body reniform and flattened, with oral region at indented part; oral cavity deep and transverse; somatic ciliation holotrichous and dense; common in anaerobic habitats (Fig. 2.17 M) ..... Plagiopylidae

2(1) Body discoidal; somatic ciliature sparse; oral cavity in posterior half 3

2′ Body quadrate or helmet-shaped, generally with short posterior spines; somatic ciliature relatively dense, in short rows at front and rear; oral cavity equatorial (Fig. 2.11 M) ..... Epalxellidae

3(2) Body smooth in outline apart from two prominent anterior spines and one posterior spine; band of cilia on ridge overhanging buccal cavity (Fig. 2.11 J) ..... Discomorphellidae

3′ Body smooth in outline without spines; somatic ciliature very sparse with longer, cirrus-like cilia at posterior end (Fig. 2.11 L) ..... Myelostomatidae

Protozoa: Ciliophora: Spirotrichea: Choreotrichia and Oligotrichia Families

1 Oral ciliature forms a closed circle ..... subclass Choreotrichia 2

1′ Oral cilature forms an open anterior collar with an anteroventral "lapel"; typically rounded or gently pointed posteriorly; somatic kineties reduced in number, forming girdles and spirals ..... subclass Oligotrichia (Fig. 2.11 V) ..... Strombidiidae

2(1) Loricate, attached to inner wall of lorica 3

2′ Not loricate 4

3(2) Delicate, gelatinous or mucoid tubular lorica, with attached debris, often translucent (Fig. 2.11 S) ..... Tintinnididae

3′ Lorica rigid, agglomerate of mineral grains and diatom fragments (Fig. 2.11 T) ..... Codonellidae

4(2) Rows of somatic ciliature equally distributed around body, extending length of body; body cilia may be long (Fig. 2.11 U) ..... Strombidinopsidae

4′ One or more usually short rows of body cilia; body ciliature short (Fig. 2.11 X) ..... Strobilidiidae

Protozoa: Ciliophora: Armophorea: Families

1 Body slightly twisted to left; long caudal spine commonly present; somatic kineties as small kineties or tufts (Fig. 2.11 R) ..... Caenomorphidae

1′ Body conspicuously contorted, anterior part twisted to left; somatic ciliation holotrichous (Fig. 2.11 K) ..... Metopidae

Protozoa: Ciliophora: Heterotrichea: Families

1 Body not trumpet-shaped 2

1′ Body trumpet-shaped; highly contractile; oral ciliature spirals clockwise around flared anterior end; often pigmented and/or with algal endosymbionts; sometimes attached to substratum (Fig. 2.10 F) ..... Stentoridae

2(1) Body not laterally compressed 3

2′ Body laterally compressed, pyriform to ellipsoid; often pigmented pink, red, or purple; long, narrow peristome on left margin; non-contractile (Fig. 2.10 B) ..... Blepharismidae

3(2) Body ovoid, ellipsoidal or elongate; oral region expansive; oral ciliature prominent 4

3′ Body often elongate, cylindrical and very contractile oral cavity shallow; peristomial area long, narrow, oral ciliature inconspicuous (Fig. 2.10 A ..... Spirostomidae

4(3) Body ovoid, often anteriorly pointed; buccal cavity occupying much of anterior part of body; peristomial field ciliated, bordered by adoral polykinetids; paroral membrane inconspicuous (Fig. 2.10 D) ..... Climacostomidae

4′ Body ellipsoidal to very elongate, contractile; paroral membrane prominent; peristomial field absent (Fig. 2.10 E) ..... Condylostomatidae

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Chapter 3

Phylum Porifera

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INTRODUCTION

Sixty-four freshwater sponge species (Porifera: Spongillida) occur in a wide variety of Palaearctic perennial and temporary aquatic habitats. These basal invertebrates have a key functional role contributing to ecosystem services by recycling suspended and dissolved organic matter, producing a notable amount of benthic biomass, and providing favorable microhabitats for bacteria, algae, fungi, protozoa, invertebrates, and vertebrates. Sponges are also bioindicators of water quality. Spongillida are not currently protected under environmental law with rare exceptions (e.g., Brazil), and no reliable data exist, due to the scarcity of studies on their conservation status (Manconi & Pronzato, 2008, 2015, 2016).

The first two freshwater sponge species were described by Linnaeus (1759) from northern Europe. The type specimen of *Spongilla lacustris* is the only still preserved Linnaean sponge (Manconi & Pronzato, 2000). The most recently described species from the Palaearctic Region (Fig. 3.1) were from Lake Baikal (Efremova, 2004) and from the Tigris River Basin (Manconi & Pronzato, 2004).

LIMITATIONS

All freshwater sponges are in the class Demospongiae, order Spongillida. Keys to families and genera are primarily based on specimens displaying all diagnostic characters, and hence care must be taken when using these characters for taxa that do not bear gemmules. For example,

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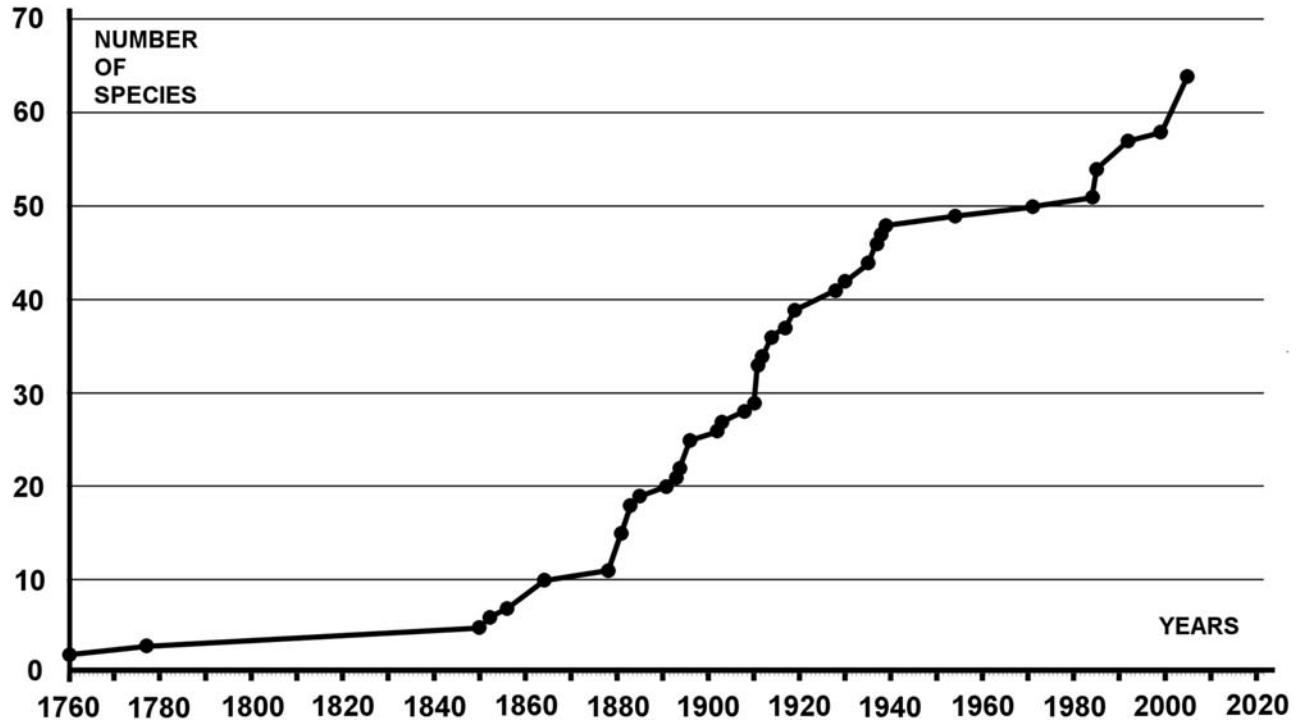


FIGURE 3.1 Order Spongillida from the Palaearctic Region. Historical trend of faunistic and taxonomic investigations focusing on descriptions of new species starting from the 1759 Linnean Systema Naturae up to the present. After a very long post-Linnean period of absence of records (c. 1770–1850) a continuous increase of new discoveries (c. 1850–1950) has been followed by a recent decrease of research. The last new Palaearctic species were all described in 2004.

specimens collected during seasons when gemmules are not produced might be erroneously identified as *incertae sedis*, or as one of the genera that do not produce gemmules. When gemmules are present, their typical spicular complement (gemmuloscleres) is diagnostic, together with the gemmular theca architecture and the spicule spatial arrangement in the skeletal network. For all freshwater sponge species reported in this chapter we supply figures showing the key diagnostic characters. Unfortunately, for several species, iconographic documentation is very scarce and quite useless.

Knowledge on Palaearctic freshwater sponges is reported in fundamental studies and monographs (Bowerbank, 1863; Czerniawsky, 1880; Vejdovsky, 1883, 1888; Weltner, 1895; Arndt, 1926; Rezvoi, 1927, 1936; Gee, 1930–31, 1931–32; Sasaki, 1934, 1936; Penney & Racek, 1968; Banarescu, 1992; Lizhen, 1998; Masuda, 1998, 2006; Pronzato & Manconi, 2001; Manconi & Pronzato, 2002, 2004, 2007, 2008, 2009; Efremova, 2004), although further investigations in inadequately explored areas should yield new taxa and new records (see Ruengsawang et al., 2016).

Only a few poriferan families (out of c. 8,400 species) live in fresh and/or brackish water and all belong to the order Spongillida Manconi & Pronzato, 2002 (Manconi et al., 2013; Manconi & Pronzato, 2015, 2016). Taxonomic richness values are continuously under revision (Manconi & Pronzato, 2007, 2008, 2015, 2016) and updated online (Van Soest et al., 2018, World Porifera Database). At present seven families, 47 genera, and 238 Spongillida species (see Manconi & Pronzato, 2015, 2016) are known from all continents except Antarctica. The Palaearctic Region hosts four families (plus *Incertae sedis*), 22 genera, and 64 species. Some taxa need revision.

Identification of Spongillida specimens to species level is based on diagnostic characters observed via light microscopy and/or scanning electron microscopy. The keys presented here are primarily based on morphotraits of the skeleton and gemmules (resistant bodies). As some species are insufficiently described, some parts of the keys are weak.

TERMINOLOGY AND MORPHOLOGY

The terminology of freshwater sponges follows Pronzato & Manconi (2001) and Manconi & Pronzato (2002, 2016). Growth form ranges from encrusting to massive or

arborescent (Fig. 3.65). Body size ranges from <1 mm to large patches up to 1 m in diameter, or c. 1 m in height for the arborescent habitus. The color in life varies from white to brown to green in different light intensities. Body consistency varies from soft to hard according to the various amount of spongin (collagen) and siliceous spicules in the skeleton. The skeleton consists of a reticulate network of siliceous spicules associated to spongin. Skeleton spicules range from large (megascleres) to small (microscleres, when present).

Most freshwater sponges produce gemmules, which are resistant bodies armed by gemmuloscleres (special microscleres) to survive and persist in potential stressing conditions (e.g., drying, freezing, anoxia). Gemmules are passive dispersal bodies, transported by water flow, wind, or organismal vectors (e.g., migrant animals). Sponges may colonize a wide array of natural and artificial substrates (Manconi & Pronzato, 2008, 2015, 2016).

Spongillida species are characterized by species-specific spicules (spicular complement), i.e., megascleres, microscleres, and gemmuloscleres protecting gemmules. In most cases, the gemmuloscleres and gemmular architecture are the primary diagnostic characters.

MATERIAL PREPARATION AND PRESERVATION

Sponge specimens can be preserved long term either by drying or in ethanol. For standard methods to characterize diagnostic traits of the spicular complement and of gemmules see Chapter 8 (Manconi & Pronzato, 2015) in volume I of this series.

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KEYS TO SPONGILLIDA

The records of *Eunapius nitens* and *Stratospongilla sumatrana* from the northern Nile River are not included because the records are dubious.

Spongillida: Families

1	Gemmules present 2
1′	Gemmules absent 4
2(1)	Gemmular theca bi- or trilayered (pneumatic layer generally present) 3
2′	Gemmular theca monolayered; gemmuloscleres, when present, short irregular strongyles (tangentially arranged); gemmules in the basal portion (for the few species known to produce them); skeletal network typically multispicular alveolate-reticulate with scanty spongin; megascleres almost exclusively strongyles, rarely oxeas; microscleres rarely present ..... Potamolepidae [Not yet known from the Palaearctic]
3(2)	Gemmuloscleres oxeas, strongyles, birotules, pseudobirotules, botryoidal, clavate (radially to tangentially arranged); skeletal network typically paucispicular irregularly reticulate; smooth or variably ornamented megascleres (oxeas and strongyles); microscleres usually present ..... **Spongillidae [p. 46]**
3′	Gemmuloscleres tubelliform, parmuliform, pseudobirotules (almost exclusively radially arranged); skeletal network typically multispicular alveolate-reticulate with scanty spongin; smooth or variably ornamented megascleres (oxeas and strongyles); microscleres usually present ..... Metaniidae [Not yet known from the Palaearctic]
4(1)	Skeletal network typically multispicular or paucispicular 5
4′	Skeletal network variously structured; megascleres smooth, spiny or tubercled oxeas; microscleres absent (endemic to ancient lakes) (Fig. 3.2) ..... Spongillida, one species: *Ohridospongilla stankovici* Gilbert & Hadzische, 1984 [Incompletely described species. Lake Ohrid]
5(4)	Skeletal network typically multispicular 6
5′	Skeletal network typically paucispicular, irregularly reticulate; megascleres spiny oxeas; microscleres absent (Fig. 3.3) ..... Metschnikowiidae, one species: *Metschnikowia tuberculata* Grimm, 1877 [Caspian Sea]
6 (5)	Skeletal network typically multispicular alveolate-reticulate, with scanty spongin; megascleres spiny oxeas to strongyles; microscleres absent ..... **Lubomirskiidae** [Lake Baikal]
6′	Skeletal network typically multispicular alveolate-reticulate, with scanty spongin; megascleres exclusively spiny or tubercled oxeas; microscleres absent ..... **Malawispongiidae** [Endemic to ancient lakes]

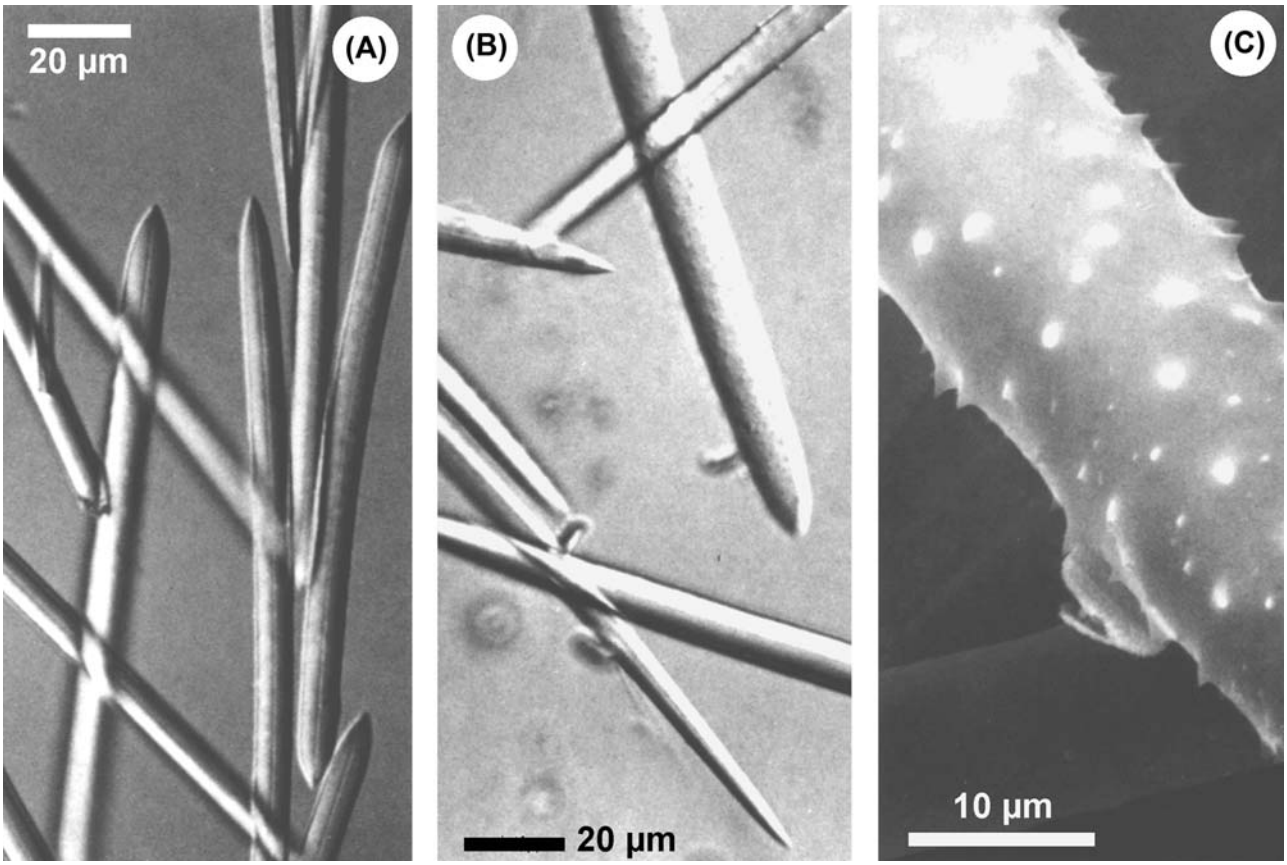


FIGURE 3.2 *Ohridospongilla stankovici* Gilbert & Hadzische, 1984. (A–B) Spiny and smooth oxeas (megascleres); (C) close-up of the spinosity of a megasclere surface. *Modified from Gilbert & Hadzische, 1984.*

Spongillida: Spongillidae: Genera

1	Birotules and pseudobirotules absent	2
1′	Birotules and pseudobirotules present	10
2(1)	Microscleres and/or gemmuloscleres present (not pseudobirotules and/or birotules)	3
2′	Complete absence of microscleres and gemmuloscleres; bare gemmule lacking pneumatic layer and gemmuloscleres; microscleres absent; megascleres spiny oxeas	***Nudospongilla* [p. 48]**
3(2)	Gemmuloscleres absent	4
3′	Gemmuloscleres present	5
4(3)	Microscleres spiny oxeas; megascleres smooth oxeas	***Spongilla*** (in part)
4′	Megascleres and microscleres spiny or completely smooth oxeas; presence of gemmular cage pneumatic gemmular layer absent or inconspicuous	***Pottsiela* [p. 58]**
5(3)	Microscleres spiny oxeas	6
5′	Microscleres absent	7
6(5)	Megascleres smooth oxeas; gemmuloscleres, when present, spiny oxeas or strongyles often very bent	***Spongilla* [p. 48]**
6′	Megascleres spiny oxeas; gemmuloscleres with tips typically botryoidal (Fig. 3.4)	*Pectispongilla subspinosa* Annandale, 1911 [Japan, Korea. Oriental Region]
7(5)	Megascleres spiny or spiny and smooth oxeas	8
7′	Megascleres smooth oxeas; gemmuloscleres oxeas and strongyles, smooth or with spiny tips, tangentially arranged on the gemmular surface	***Eunapius* [p. 58]**

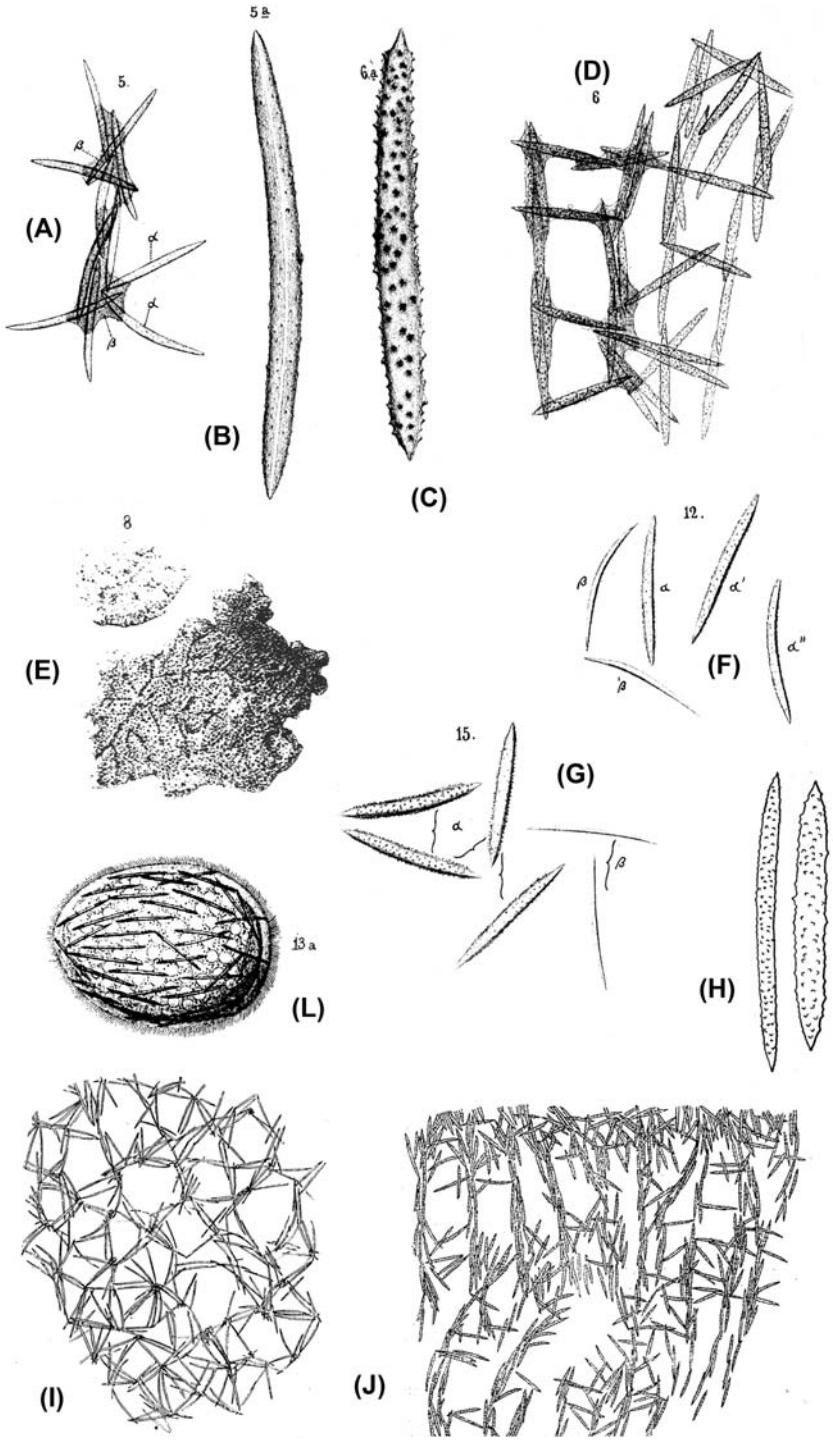


FIGURE 3.3 *Metschnikowia tuberculata* Grimm, 1877. (A, D, I, and J) Skeletal network; (B, C, F, G, and H) spiny oxeas; (E) drawing of a fresh specimen; (L) larva. *Modified from Dybowski, 1880 and Koltun, 1962.*

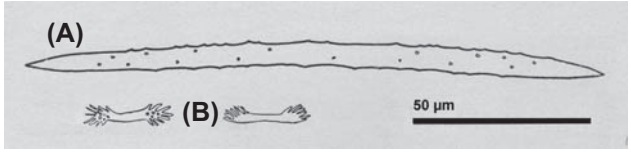


FIGURE 3.4 *Pectispongilla subspinosa* Annandale, 1911. (A) Spiny oxea (megasclere); (B) gemmuloscleres. *Modified from Penney & Racek, 1968.*

8(7)	Megascleres spiny oxeas	9
8′	Megascleres spiny and smooth oxeas; gemmuloscleres of two morphs: strongyles stout, short, and spiny, tangentially embedded in the outer layer of gemmular theca; spiny oxeas abruptly pointed, radially arranged in between the inner and outer layers ... ***Stratospongilla*** **[p. 62]**	
9(8)	Gemmuloscleres with 2–9 spiny axes and rounded or tricuspidate tips embedded radially in the gemmular theca (Fig. 3.5) ... *Sanidastra yokotonensis* Volkmer-Ribeiro & Watanabe, 1983 [Japan. France: Corsica. Italy: Sardinia]	
9′	Gemmuloscleres spiny strongyles radially arranged ... ***Radiospongilla*** **[p. 65]**	
10(1)	Birotules with rotules bearing spiny to indented edges, generally associated with pseudobirotules	11
10′	Birotules with rotules bearing smooth edges, pseudobirotules absent; microscleres absent; megascleres oxeas very spiny; gemmuloscleres smooth birotules radially arranged ... ***Trochospongilla*** **[p. 69]**	
11(10)	Birotules and/or pseudobirotules present, exclusively as gemmuloscleres	12
11′	Pseudobirotules present, exclusively as microscleres; gemmuloscleres spiny oxeas and/or strongyles tangentially arranged on gemmular theca; megascleres smooth to microgranulate; microscleres pseudobirotules with smooth shaft ... ***Corvospongilla*** **[p. 71]**	
12(11)	Gemmuloscleres birotules of a single morph	13
12′	Gemmuloscleres birotules and/or pseudobirotules belonging to two morphs (birotules + pseudobirotules or birotules + spiny oxeas)	14
13(12)	Birotules with short shaft (usually less than twice the rotule diameter); microscleres absent; megascleres microspiny and/or smooth oxeas ... ***Ephydatia*** **[p. 71]**	
13′	Birotules with long spiny shaft (2–3 times the rotule diameter); microscleres absent; microspiny megascleres, rare smooth oxeas (Fig. 3.6) ... *Umborotula bogorensis* (Weber, 1890) [Japan, China, Korea. Australian and Oriental regions]	
14(11)	Gemmuloscleres birotules (long shaft) and pseudobirotules (long shaft) radially arranged; microscleres spiny oxeas; megascleres spiny oxeas ... ***Heteromeyenia*** **[p. 78]**	
14′	Gemmuloscleres birotules (short shaft) and pseudobirotules (long and spiny shaft) radially arranged; microscleres absent; megascleres spiny oxeas (Fig. 3.7) ... *Racekiela ryderi* (Potts, 1882) [Holarctic]	

Spongillida: Spongillidae: *Nudospongilla*: Species

1	Megascleres smooth oxeas	2
1′	Megascleres spiny oxeas (Fig. 3.8) ... *Nudospongilla coggini* (Annandale, 1910) [China: Yunnan]	
2(1)	Megascleres slim, abruptly pointed smooth oxeas (300 × 10 µm) (Fig. 3.9) ... *Nudospongilla ehraiensis* Lizhen, 1998 [China: Yunnan]	
2′	Megascleres stubby, slender nearly straight oxeas (250 × 15 µm) (Fig. 3.10) ... *Nudospongilla yunnanensis* (Annandale, 1910) [Incompletely described species. China: Yunnan]	

Spongillida: Spongillidae: *Spongilla*: Species

The description of *Spongilla chaohuensis* Cheng, 1991 from Hebei (China) is incomplete and without illustrations.

1	Megascleres spiny and smooth oxeas	2
1′	Megascleres smooth oxeas	3
2(1)	Megascleres and microscleres spiny oxeas; gemmuloscleres spiny strongyles often with inflated tips (Fig. 3.11) ... *Spongilla prespensis* Hadzische, 1953 [Lake Prespa, Macedonia?]	
2′	Megascleres smooth and spiny oxeas; microscleres and gemmuloscleres spiny oxeas (Fig. 3.12) ... *Spongilla stankovici* Arndt, 1938 [Lake Ohrid]	
3(1)	Microscleres spiny oxeas and/or strongyles	4
3′	Microscleres (gemmuloscleres?) smooth oxeas often with bifid (or more) tips (Fig. 3.13) ... *Spongilla jiujiangensis* Cheng, 1991 [Incompletely described species. China: Hebei]	
4(3)	Gemmuloscleres with strongly bent spines	5
4′	Gemmuloscleres strongyles (50–101 × 3–4 µm) with few scattered spines (Fig. 3.14) ... *Spongilla shikaribensis* Sasaki, 1934 [Japan]	

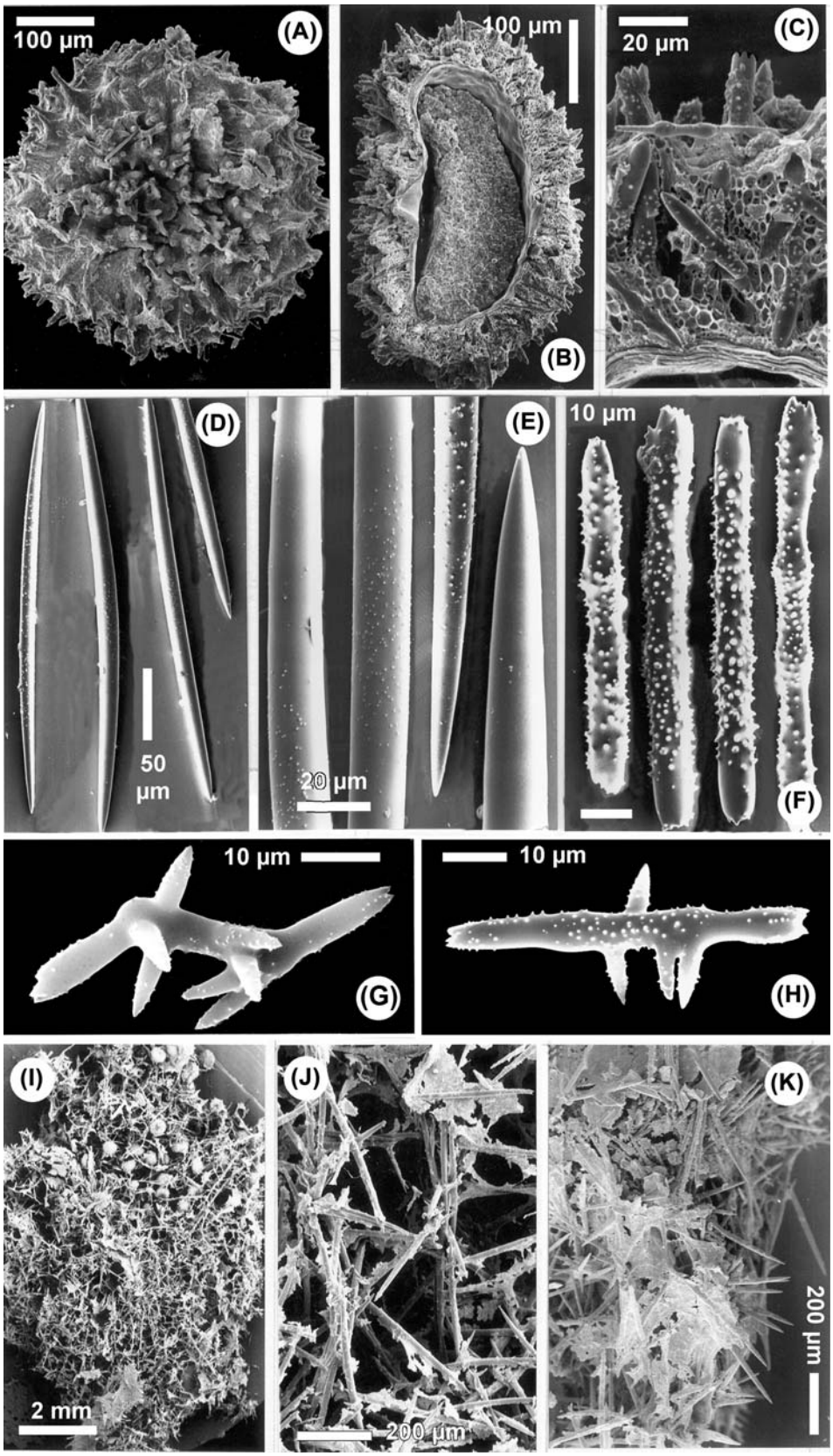


FIGURE 3.5 *Sanidastra yokotonensis* Volkmer-Ribeiro & Watanabe, 1983. (A) Gemmule with foramen (middle); (B) gemmule (cross-section) with foramen (left); (C) trilayered theca with spicules and sublayered inner layer of compact spongin (bottom); (D–E) spiny and smooth oxeas (megascleres); (F–H) gemmuloscleres; (I) skeletal network with gemmules; (J–K) skeletal network. *Modified from Manconi & Pronzato, 2002.*

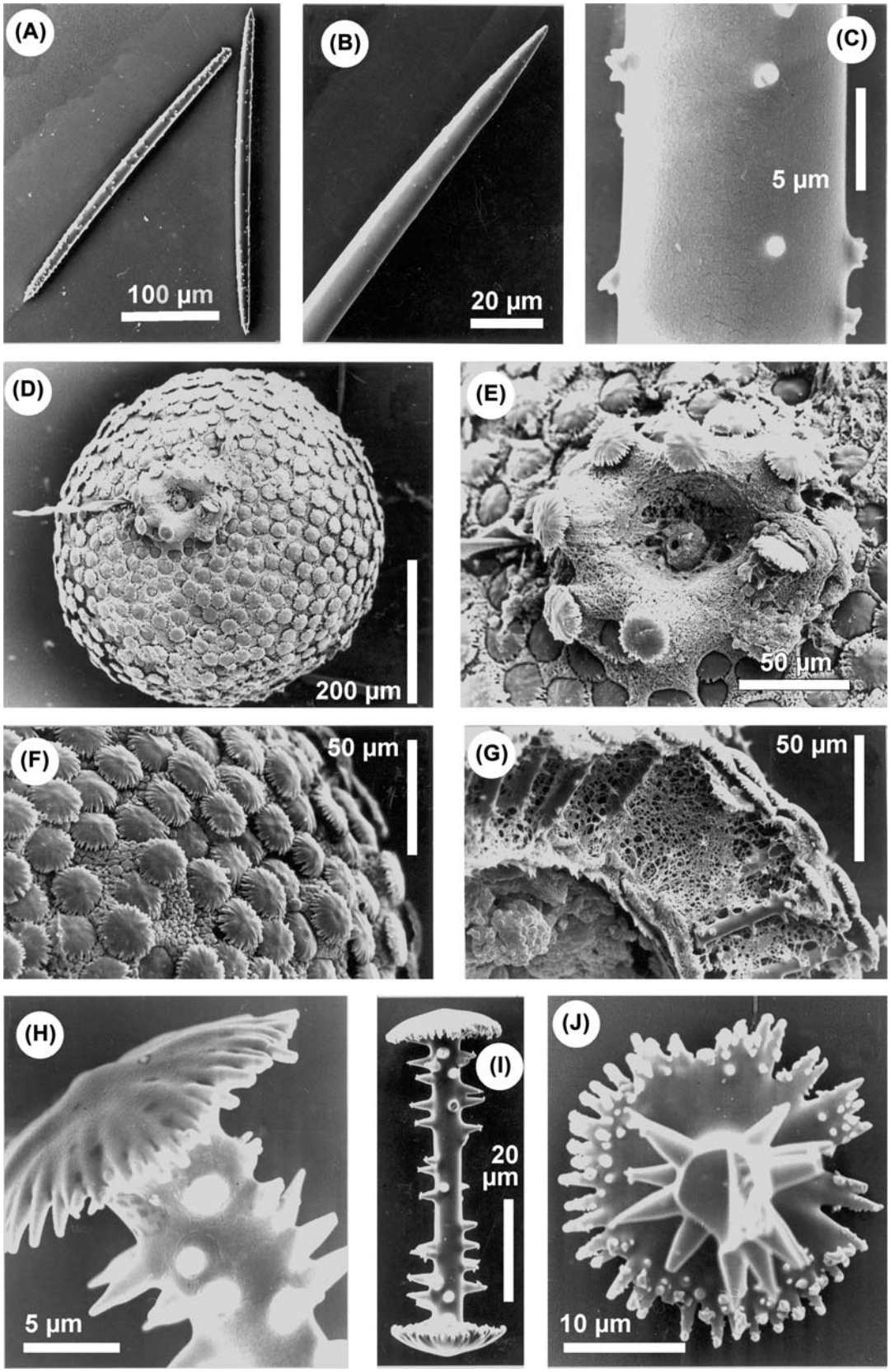


FIGURE 3.6 *Umborotula bogorensis* (Weber, 1890). (A and C) spiny oxeas (megascleres); (B) smooth oxea (megasclere); (D) gemmule with foramen; (E) foraminal area; (F) gemmular outer layer surface pierced by distal rotule of gemmuloscleres; (G) trilayered gemmular theca with radial birotule gemmuloscleres (cross-section); (H–J) gemmuloscleres. *Modified from Manconi & Pronzato, 2002.*

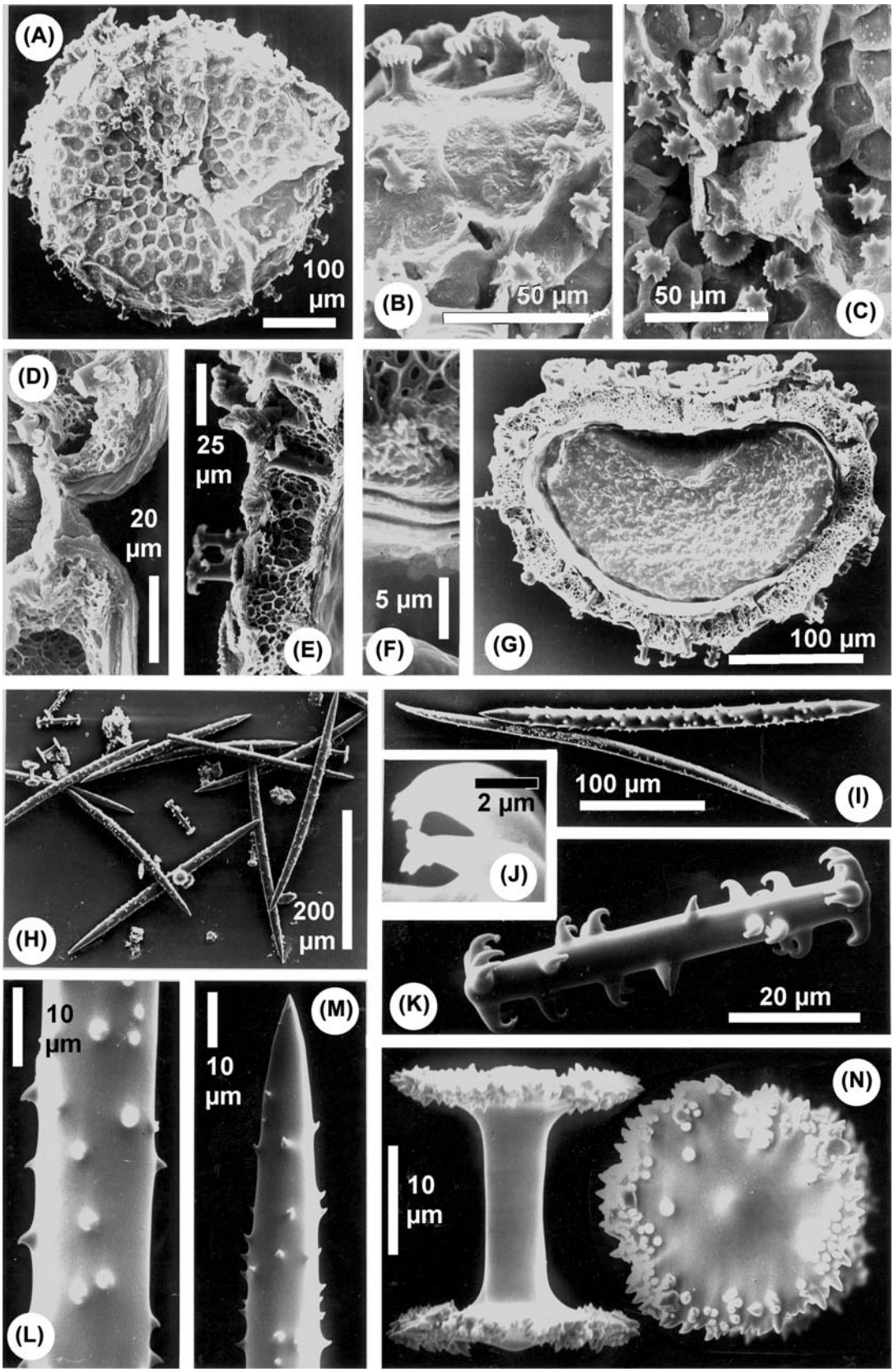


FIGURE 3.7 *Racekiela ryderi* (Potts, 1882). (A) Gemmule; (B) gemmular surface (detail); (C) foramen; (D) foramen (cross-section); (E) trilayered gemmular theca; (F) multilayered inner layer; (G) gemmular theca (cross-section); (H) spicular complement of spiny oxeas and two types of gemmuloscleres (pseudobirotule and birotule); (I) spiny megascleres; (J) microspines of a pseudobirotule (gemmulosclere); (K) pseudobirotule (gemmulosclere); (L) oxea spiny surface (megasclere); (M) oxea tip; (N) birotules (gemmuloscleres). *Modified from Manconi & Pronzato, 2002.*

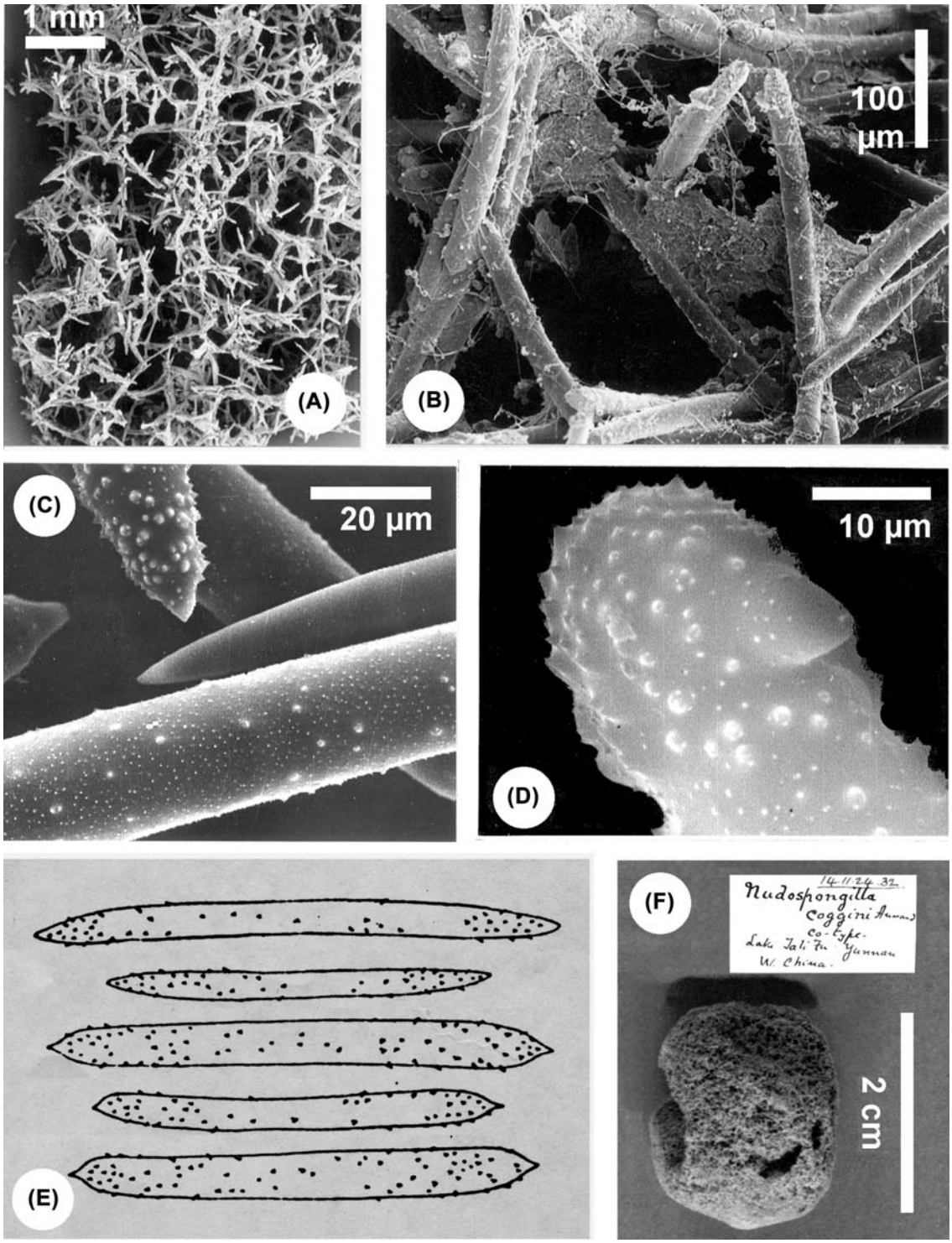


FIGURE 3.8 *Nudospongilla coggini* (Annandale, 1910). (A–B) Skeletal architecture (different magnification); (C–D) microtraits of tips and shafts (detail) of spiny oxeas (megascleres) with two types of spines; (E) spiny oxeas (megascleres); (F) cotype specimen BMNH14.11.24.32 (Natural History Museum London, dry collection). *(A–D, and F) Modified from Manconi & Pronzato, 2002; (E), modified from Annandale 1910.*

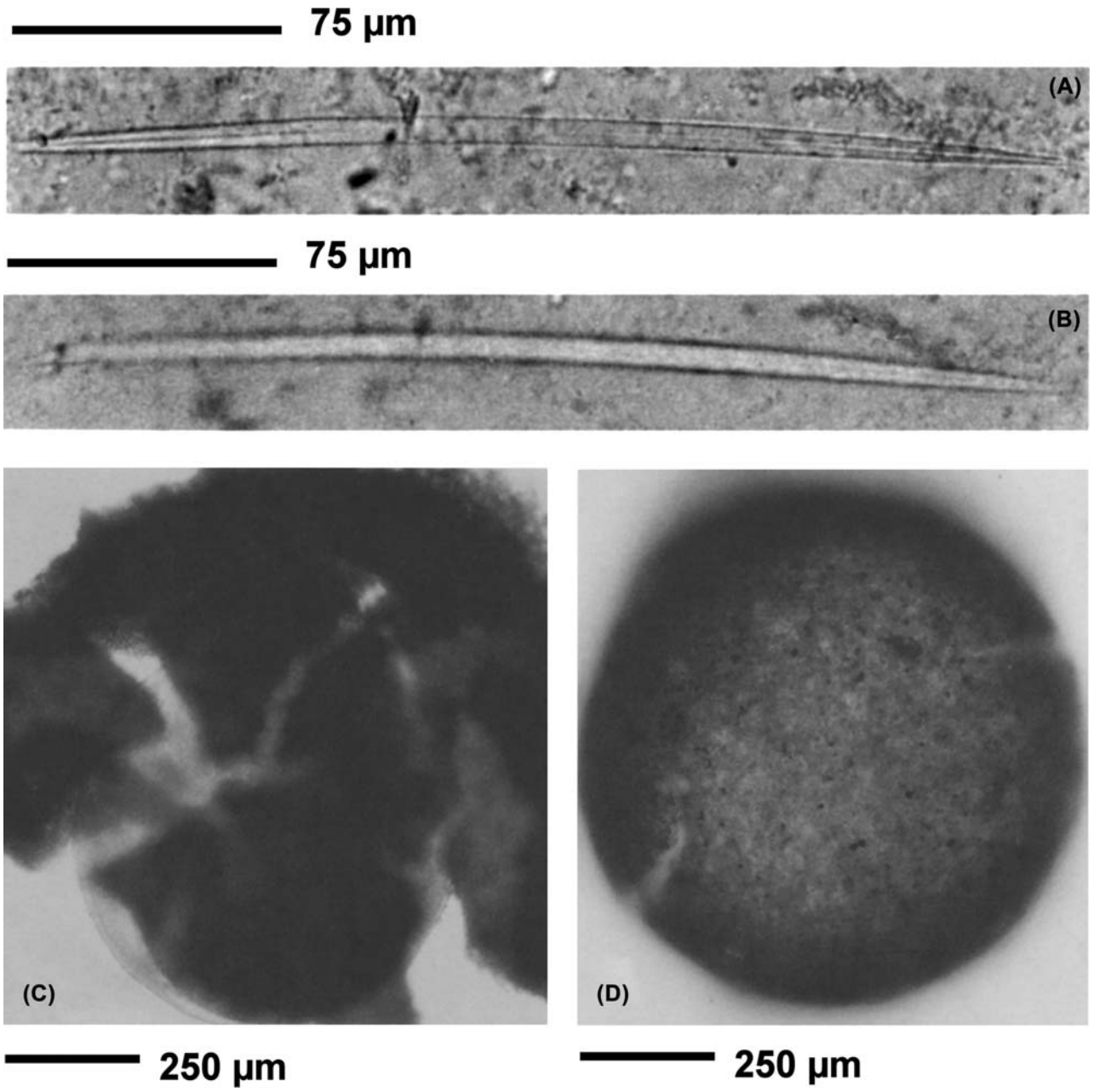


FIGURE 3.9 *Nudospongilla ehraiensis* Lizhen, 1998. (A–B) Smooth oxeas (skeletal megascleres); (C–D) gemmules. *Modified from Lizhen, 1998.*

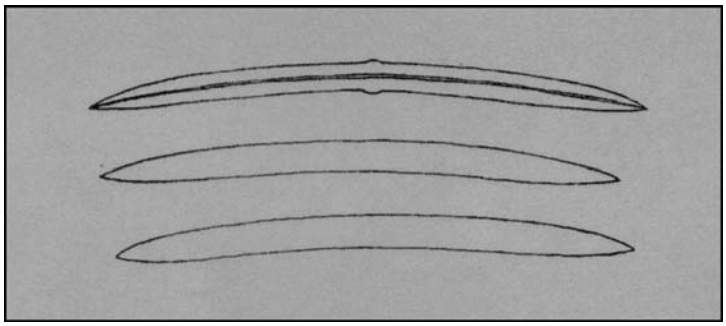


FIGURE 3.10 *Nudospongilla yunnanensis* (Annandale, 1910). Oxeas (skeletal megascleres). *Modified from Annandale, 1910.*

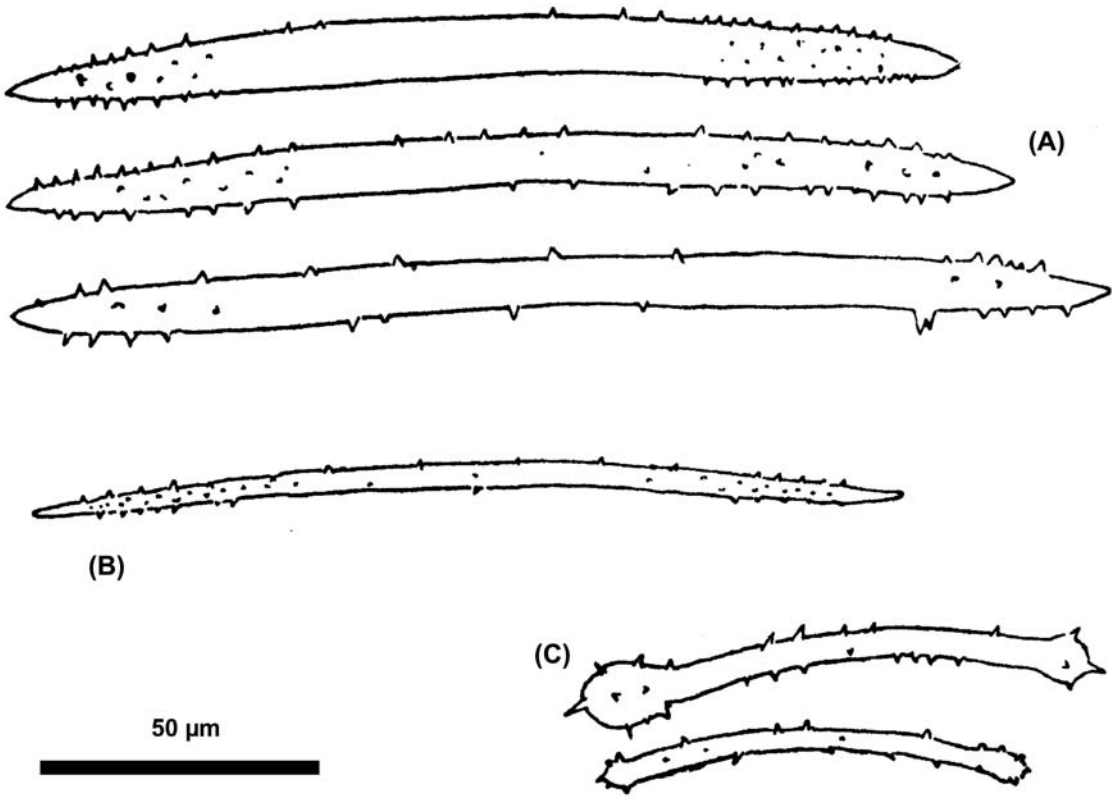


FIGURE 3.11 *Spongilla prespensis* Hadzische, 1953. (A) Spiny oxeas (reported as megascleres); (B) slim spiny oxeas (reported as microscleres; (C) smaller spiny tylotes (second type of microscleres). *Modified from Hadzische, 1953.*

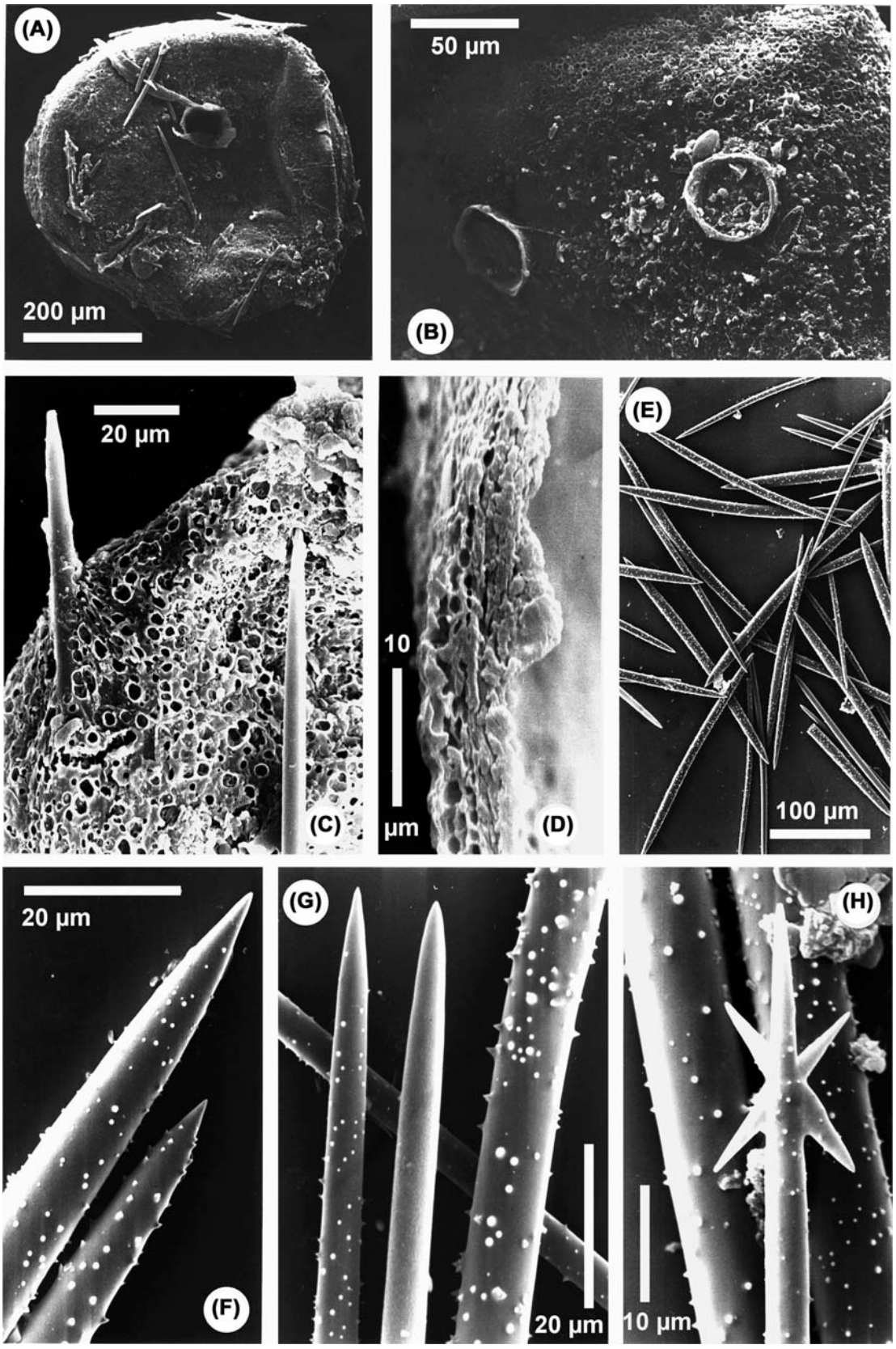


FIGURE 3.12 *Spongilla stankovici* Arndt, 1938. (A) Gemmule; (B) two foramina on the gemmular surface; (C) gemmular theca with embedded megascleres; (D) bi- to trilayered gemmular theca (cross-section); (E) spiny oxeas (megascleres); (F) spiny tips (megascleres); (G) smooth to spiny oxeas (megasclere); (H) aberrant star-shaped megasclere tip. *Modified from Pronzato & Manconi, 2001.*

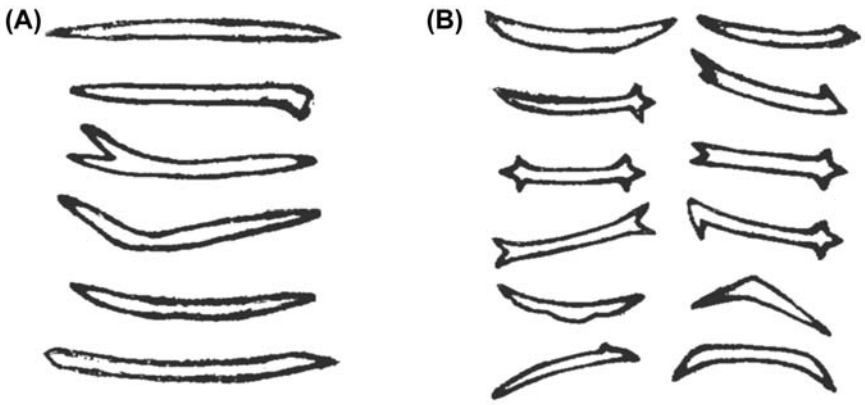


FIGURE 3.13 *Spongilla jiujiangensis* Cheng, 1991. Spicular complement. (A) Megascleres; (B) gemmuloscleres. *Modified from Cheng, 1991.*

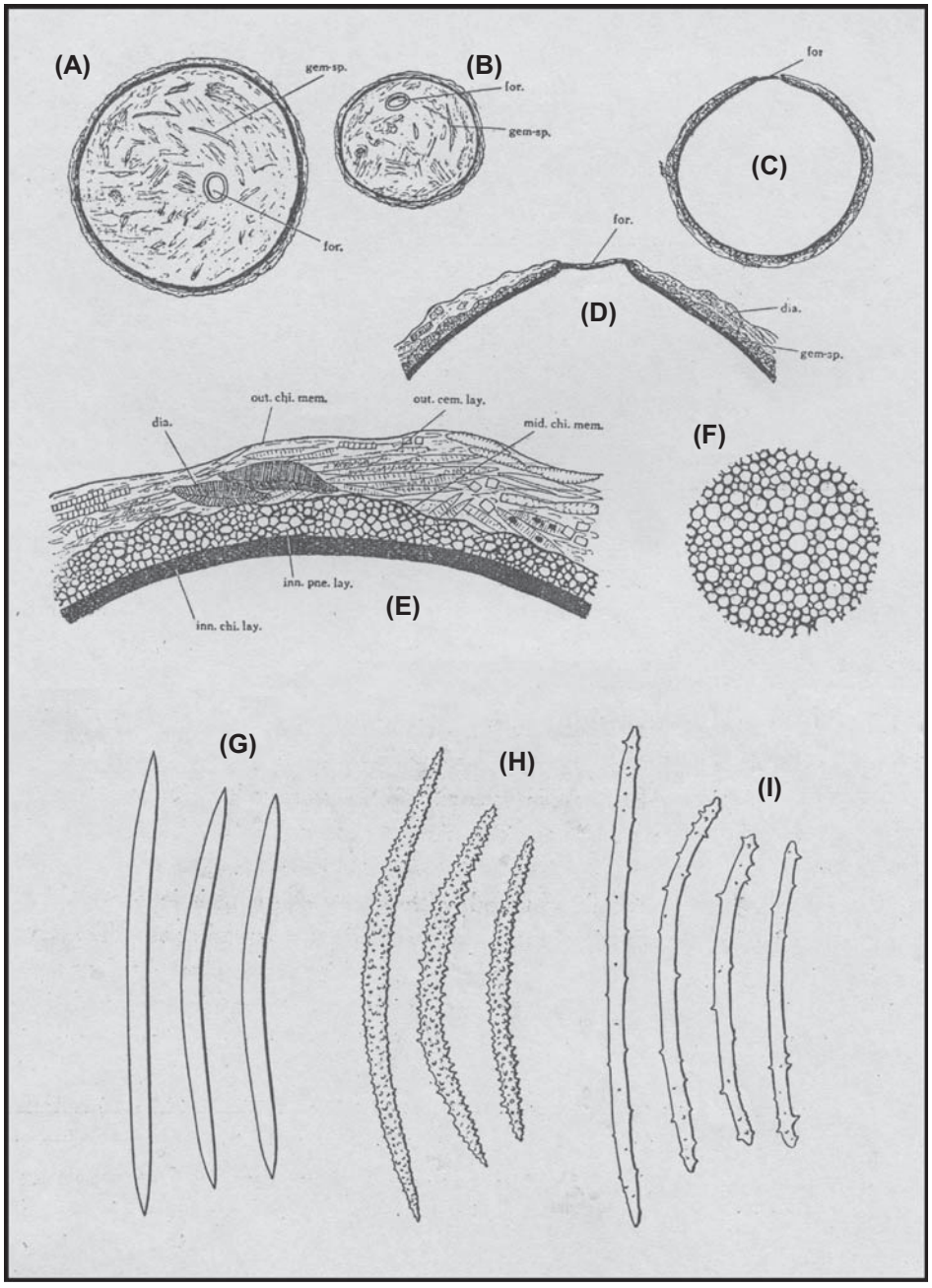


FIGURE 3.14 *Spongilla shikaribensis* Sasaki, 1934. (A–B) Gemmules with foramen; (C) gemmule (cross-section); (D) gemmule at the foramen level (cross-section); (E) gemmular multilayered theca; (F) pneumatic layer architecture (close up); (G), oxeas (megascleres); (H) spiny oxeas (microscleres); (I) gemmuloscleres; (not to scale). *Modified from Sasaki, 1934.*

5(4) Gemmuloscleres slightly to strongly bent oxeas to strongyles (18–130 × 1–10 µm) usually with strong, bent spines more dense at tips (Fig. 3.15) ..... *Spongilla lacustris* (Linnaeus, 1759)
[Widespread: Palaearctic, Nearctic regions]

5′ Gemmuloscleres strongyles (78–130 × 5–10 µm) with spines more dense at tips as distinct clavate heads, but not pseudorotules (Fig. 3.16) ..... *Spongilla alba* Carter, 1849
[Turkey. Widespread: Afrotropical, Australian, Neotropical, and Oriental regions]

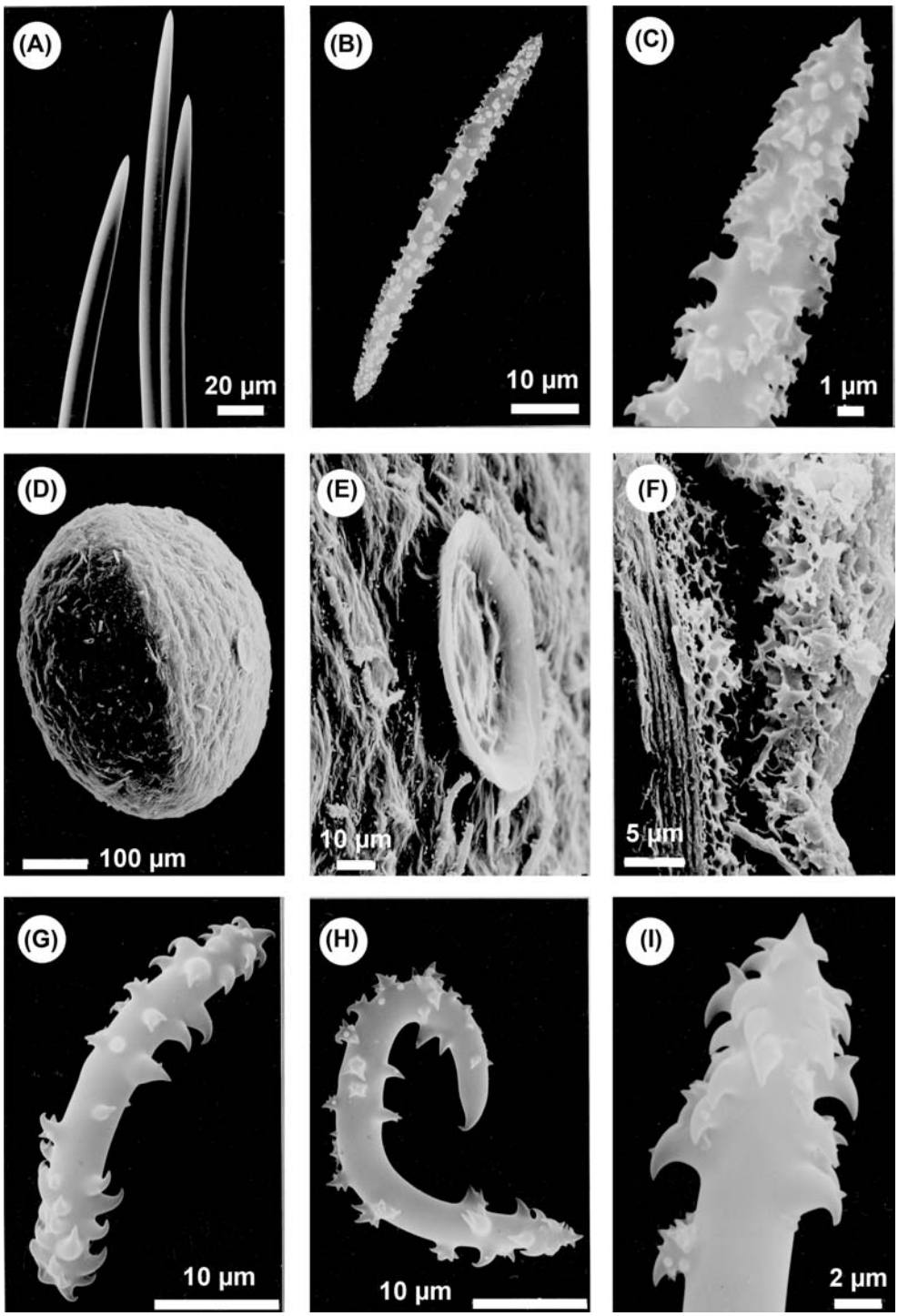


FIGURE 3.15 *Spongilla lacustris* (Linnaeus, 1759). (A) Smooth oxeas (megascleres); (B–C) spiny oxeas (microscleres); (D) gemmule armed by a few gemmuloscleres; (E) foramen with collar; (F) trilayered gemmular theca with thick pneumatic layer of chambered spongin; (G–I) spiny oxeas (gemmuloscleres). *Modified from Pronzato & Manconi, 2001.*

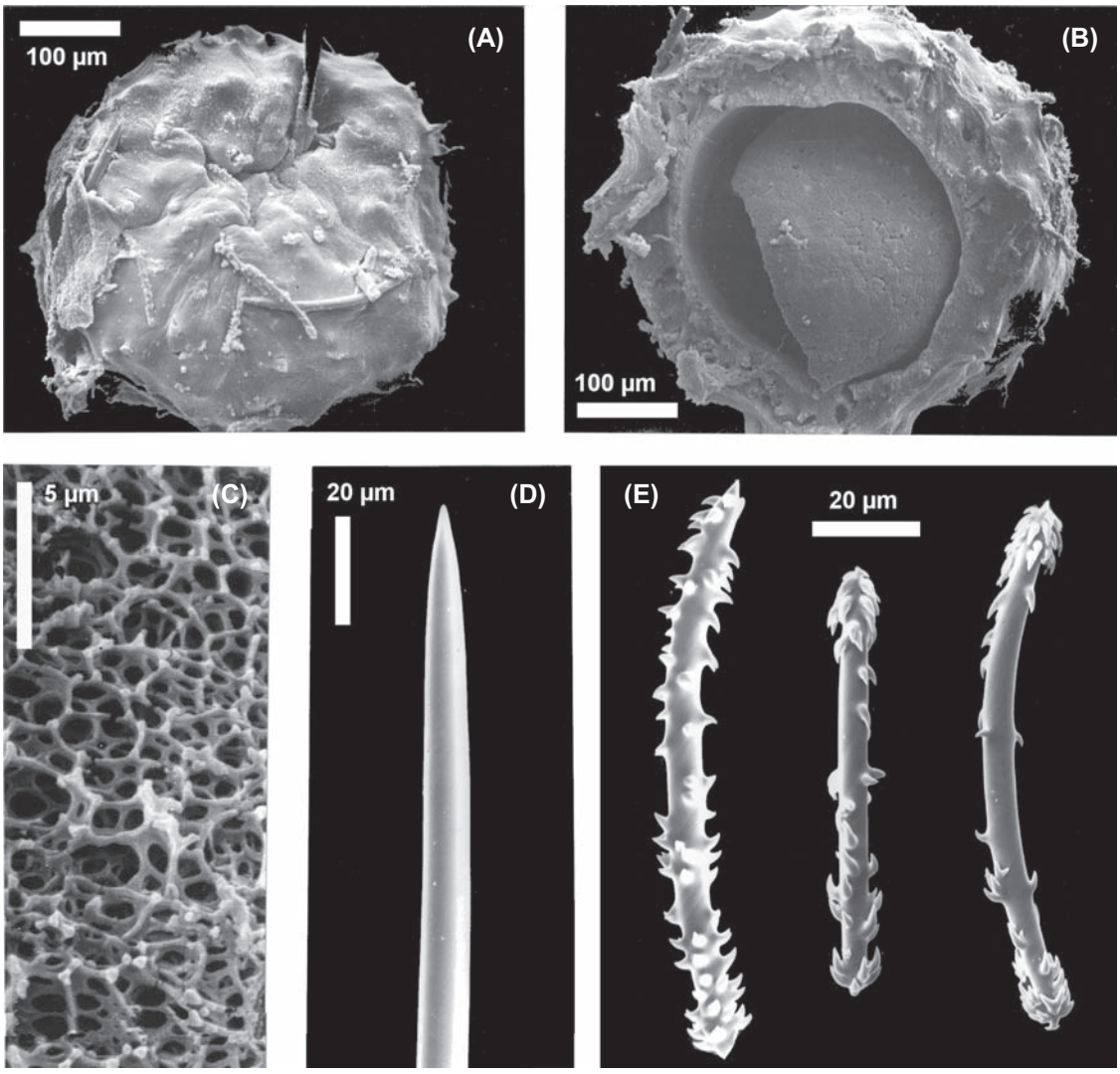


FIGURE 3.16 *Spongilla alba* Carter, 1849. (A) Gemmule; (B) gemmular theca (cross-section); (C) fibrous pneumatic layer; (D) tip of smooth oxea (megasclere); (E) gemmuloscleres.

Spongillida: Spongillidae: *Pottsiela*: Species

Two poorly described species.

1 Megascleres (155–215 µm) and microscleres (30–42 µm) entirely smooth oxeas; gemmules (450–700 µm in diameter) with cage, pneumatic layer absent or inconspicuous (Fig. 3.17) ..... *Pottsiela aspinosa* (Potts, 1880) [China. Nearctic]

1′ Megascleres (158–290 µm) entirely smooth oxeas; microscleres (50–79 µm) oxeas with minute spines; gemmules (280–750 µm in diameter) with cage, pneumatic layer absent or inconspicuous (Fig. 3.18) ..... *Pottsiela inarmata* (Annandale, 1918) [Japan]

Spongillida: Spongillidae: *Eunapius*: Species

1 Pneumatic layer present; megascleres smooth oxeas 2

1′ Gemmular theca monolayered of compact spongin; megascleres spiny oxeas (Fig. 3.19) .... *Eunapius subterraneus* Sket & Velikonja, 1984 [Croatia]

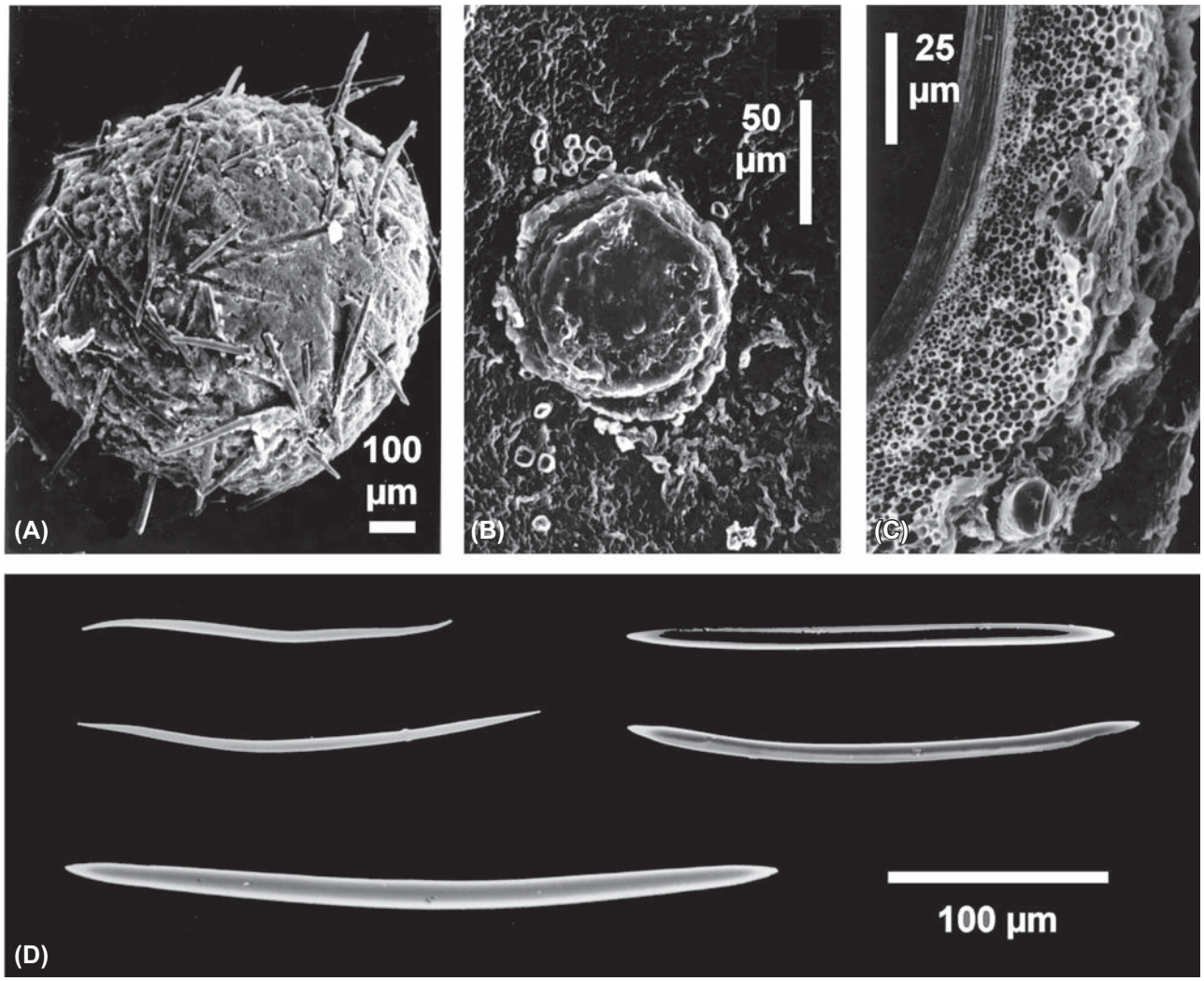


FIGURE 3.17 *Pottsiela aspinosa* (Potts, 1880). (A) Gemmule; (B) gemmular foramen; (C) trilayered gemmular theca with pneumatic layer (cross-section); (D) spicular complement.

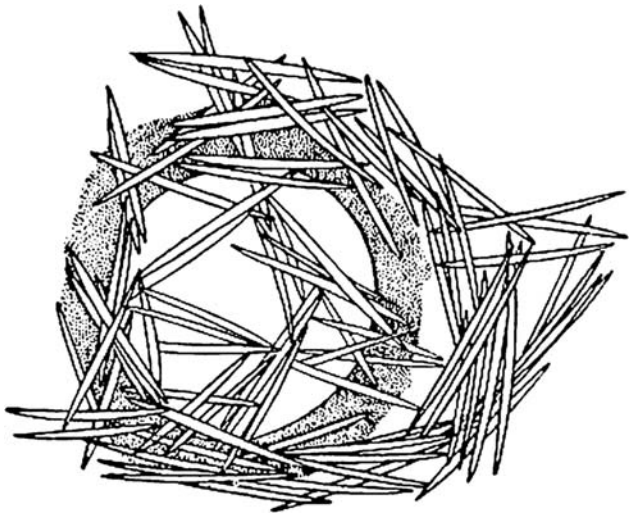


FIGURE 3.18 *Pottsiela inarmata* (Annandale, 1918). Gemmule protected by a cage of skeletal spicules (oxeas). *Modified from Annandale, 1918.*

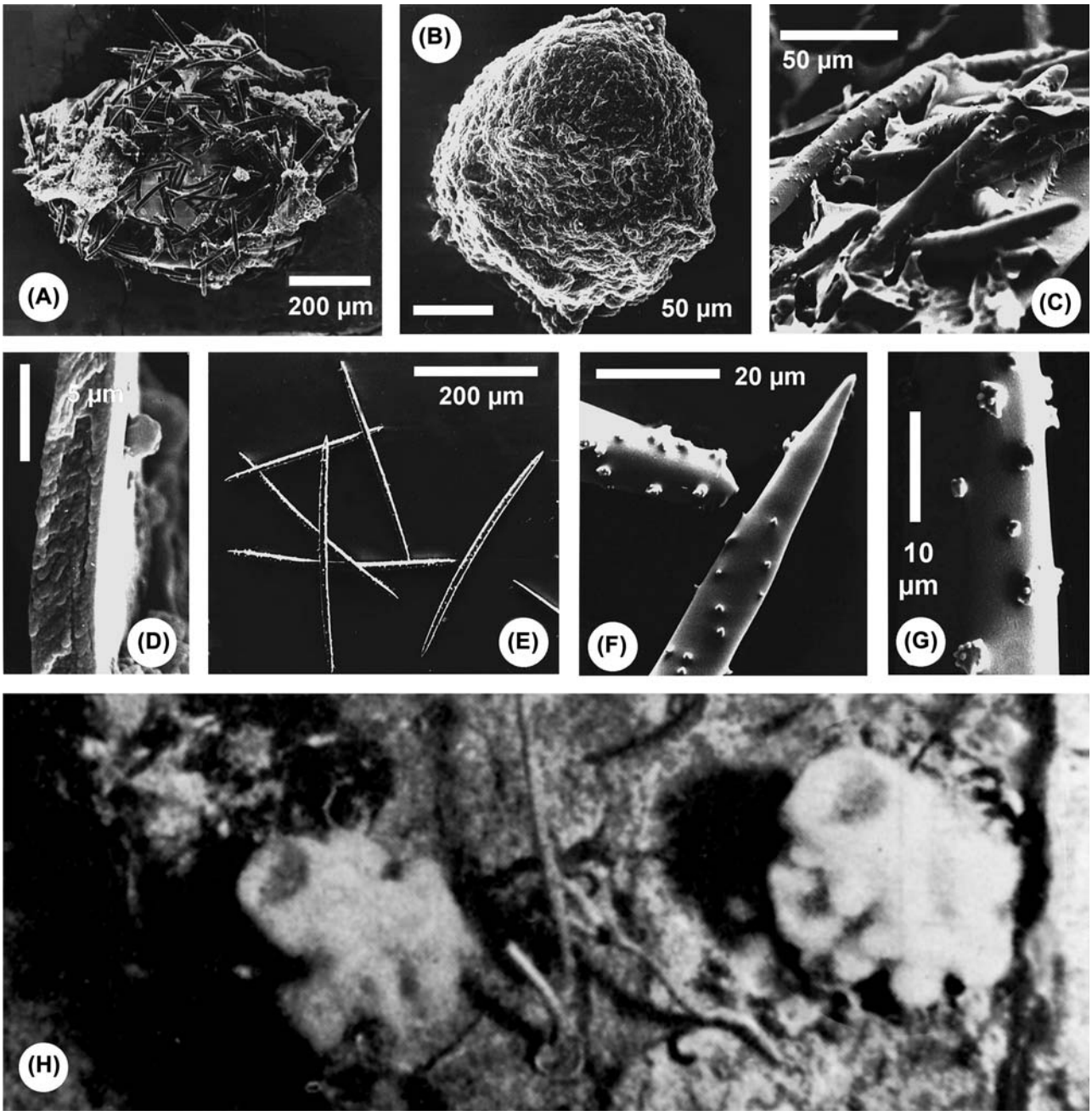


FIGURE 3.19 *Eunapius subterraneus* Sket & Velikonja, 1984. (A) Gemmule with cage; (B) gemmule; (C) gemmular cage (detail); (D) monolayered theca of compact spongin; (E) gemmular cage of tangential megascleres (detail); (F–G) spiny oxeas (megascleres); (H) two whitish specimens in a dark cave. *(A–F) Modified from Pronzato & Manconi, 2001; (H) modified from Sket & Velikonja, 1984.*

2(1)	Gemmuloscleres only as smooth oxeas	3
2′	Gemmuloscleres smooth oxeas and/or spiny strongyles and/or spiny oxeas	4
3(2)	Pneumatic layer uniformly very thick (Fig. 3.20) [Eastern Europe. Widespread: Afrotropical, Neotropical, Oriental regions]	*Eunapius carteri* (Bowerbank, 1863)
3′	Pneumatic layer very thick at the foramen level (as protruding conus) (Fig. 3.21) [China. Korea. Singapore]	*Eunapius conifer* (Annandale, 1916)
4(2)	Gemmuloscleres only spiny strongyles or spiny oxeas	5

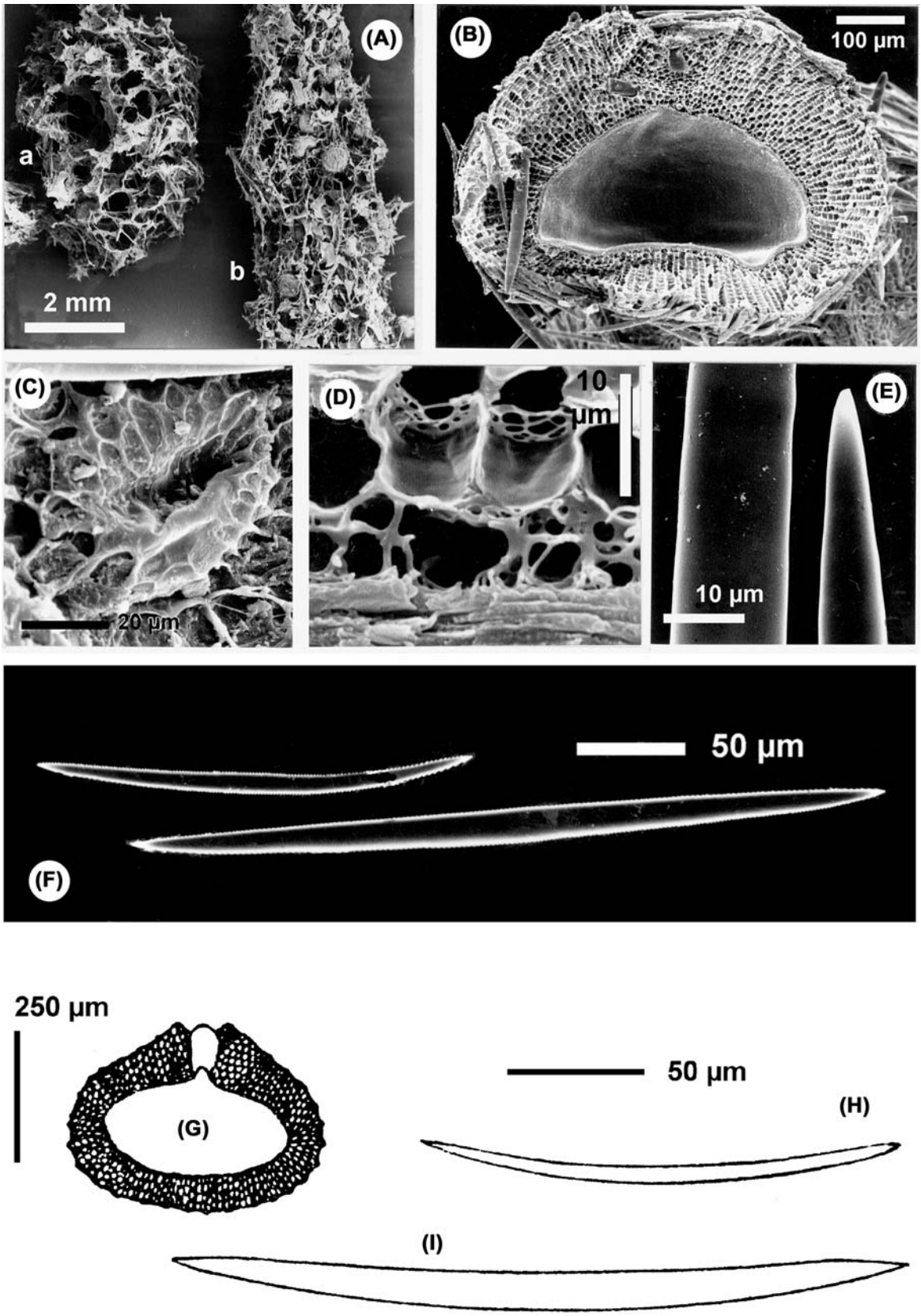


FIGURE 3.20 *Eunapius carteri* (Bowerbank, 1863). (Aa) Sponge fragment (top view); (Ab) sponge (cross-section) with gemmules (sponge surface on the right); (B) gemmular theca with thick pneumatic layer (cross-section); (C) foramen; (D) pneumatic layer (detail); (E) tip and shaft of oxeas; (F) smooth oxeas; (G) gemmular theca (cross-section); (H–I) smooth oxeas. *(A–F) Modified from Manconi & Pronzato, 2002; (G–I) modified from Penney & Racek, 1968.*

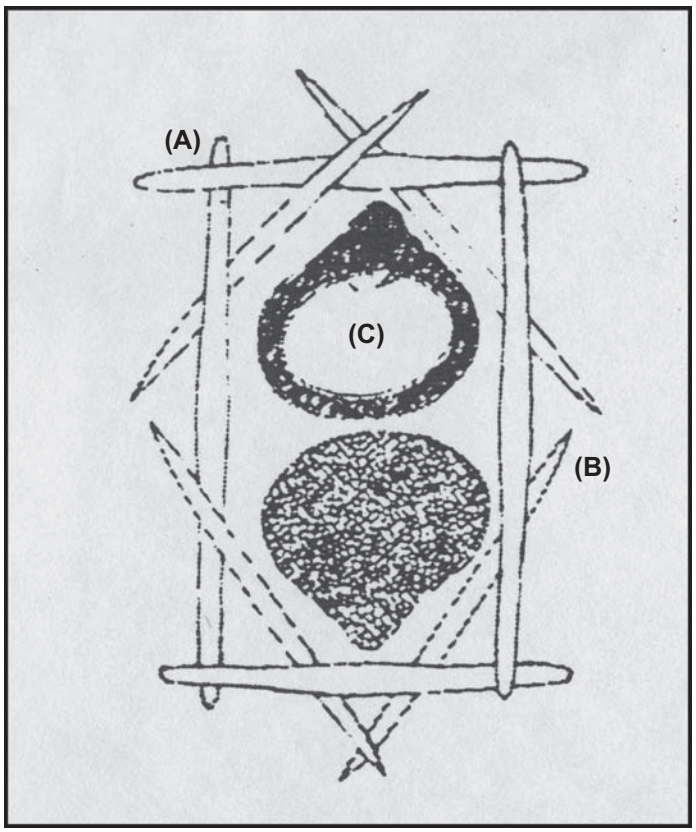


FIGURE 3.21 *Eunapius conifer* (Annandale, 1916). Pictorial representation of the spicular complement. (A) Gemmuloscleres; (B) megascleres; (C) gemmule with conical foraminal area and gemmular theca (cross-section) (not to scale). *Modified from Gee, 1927.*

4′	Gemmuloscleres spiny or smooth strongyles and/or oxeas	6
5(4)	Gemmuloscleres only spiny strongyles (Fig. 3.22) ..... *Eunapius fragilis* (Leidy, 1851) [Cosmopolitan (apparently); probable species complex]	
5′	Gemmuloscleres with few spiny oxeas (Fig. 3.23) ..... *Eunapius geei* (Annandale, 1918) [China]	
6(5)	Gemmuloscleres smooth oxeas to spiny strongyles	7
6′	Gemmuloscleres abundant, smooth to spiny oxeas (Fig. 3.24) ..... *Eunapius sinensis* (Annandale, 1910) [China, Korea, Russia. Australia]	
7(6)	Gemmuloscleres smooth oxeas on the outer gemmular layer, spiny strongyles tangentially embedded in the inner layer (Fig. 3.25) ..... *Eunapius aetheriae* (Annandale, 1913) [Northern Egypt]	
7′	Gemmuloscleres smooth oxeas and spiny strongyles embedded in both outer and inner gemmular layers (Fig. 3.26) ..... *Eunapius ryuensis* (Sasaki, 1970) [Japan. Korea]	

Spongillida: Spongillidae: *Stratospongilla*: Species

1	Microscleres absent; megascleres smooth oxeas and strongyles (230−275 × 19−21 μm); gemmuloscleres smooth strongyles (52−56 × 3−4 μm); spicules sometimes finely spiny (Fig. 3.27) ..... *Stratospongilla clementis* (Annandale, 1909) [China, Japan. Oriental and Afrotropical regions]	
1′	Microscleres as immature megascleres; megascleres smooth and spiny oxeas (310−360 × 20−30 μm); gemmules and gemmuloscleres not reported (Fig. 3.28) ..... *Stratospongilla akanensis* (Sasaki, 1934) [Japan]	

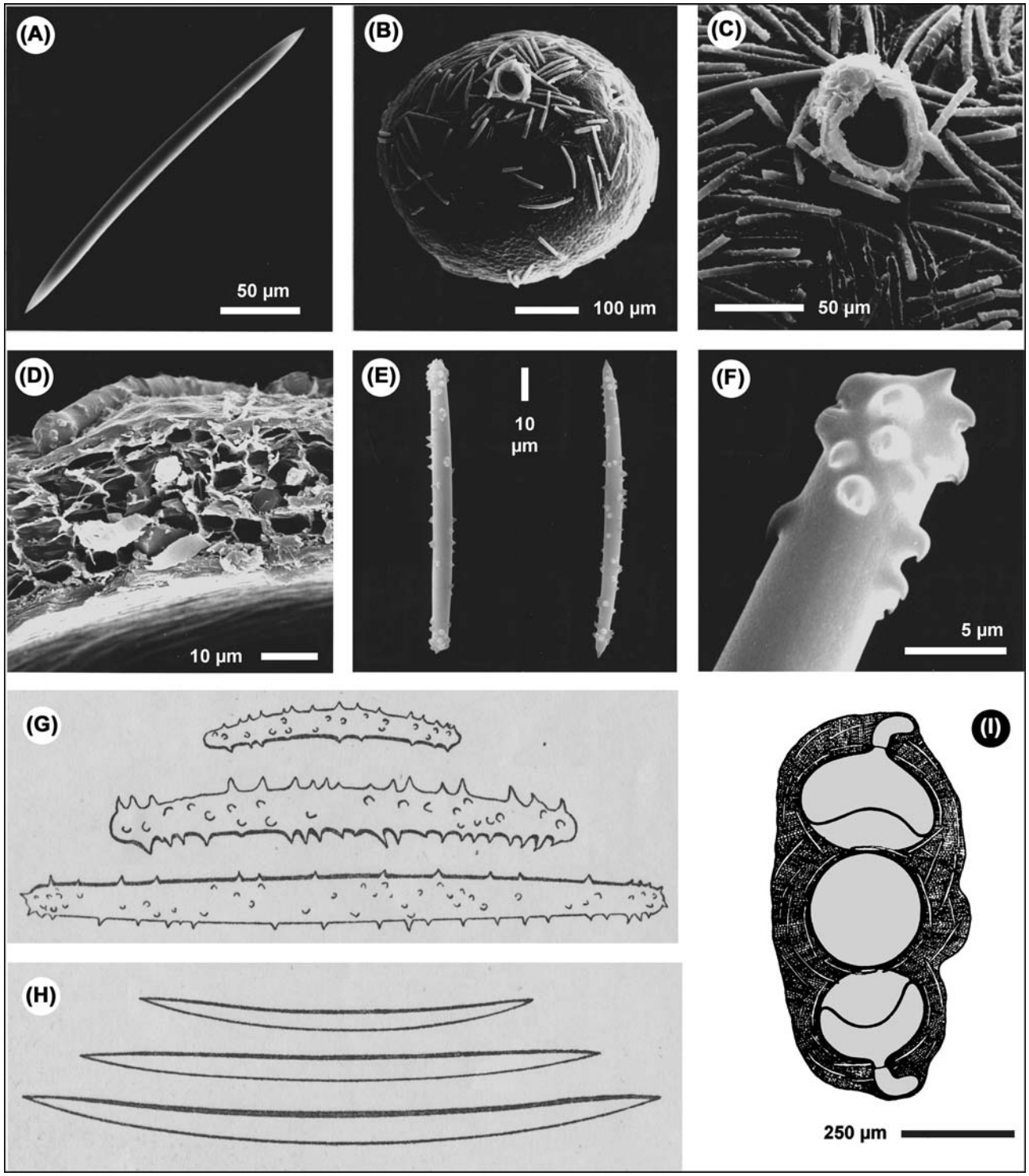


FIGURE 3.22 *Eunapius fragilis* (Leidy, 1851). (A) Smooth oxea (megasclere); (B) gemmule with foramen; (C) gemmular foramen (top view); (D) trilayered pneumatic theca (cross-section); (E) gemmuloscleres spiny strongyle (left) and spiny oxea (right); (F) strongyle with spiny tip (gemmulosclere); (G) gemmuloscleres; (H), megascleres; (I) pneumatic layer shared by a multigemmular group. *(A–F) Modified from Pronzato & Manconi, 2001; (G–H) modified from Sasaki, 1939; (I) modified from Penney & Racek, 1968.*

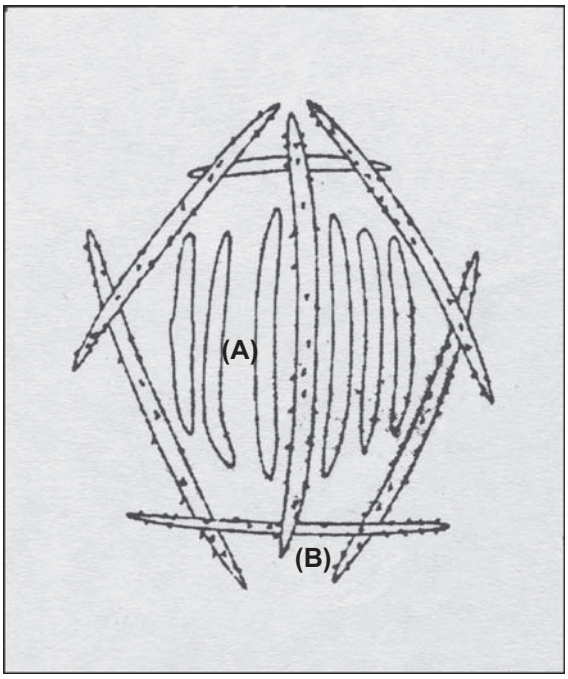


FIGURE 3.23 *Eunapius geei* (Annandale, 1918). Pictorial representation of the spicular complement. (A) Megascleres; (B) gemmuloscleres (not to scale). *Modified from Gee, 1927.*

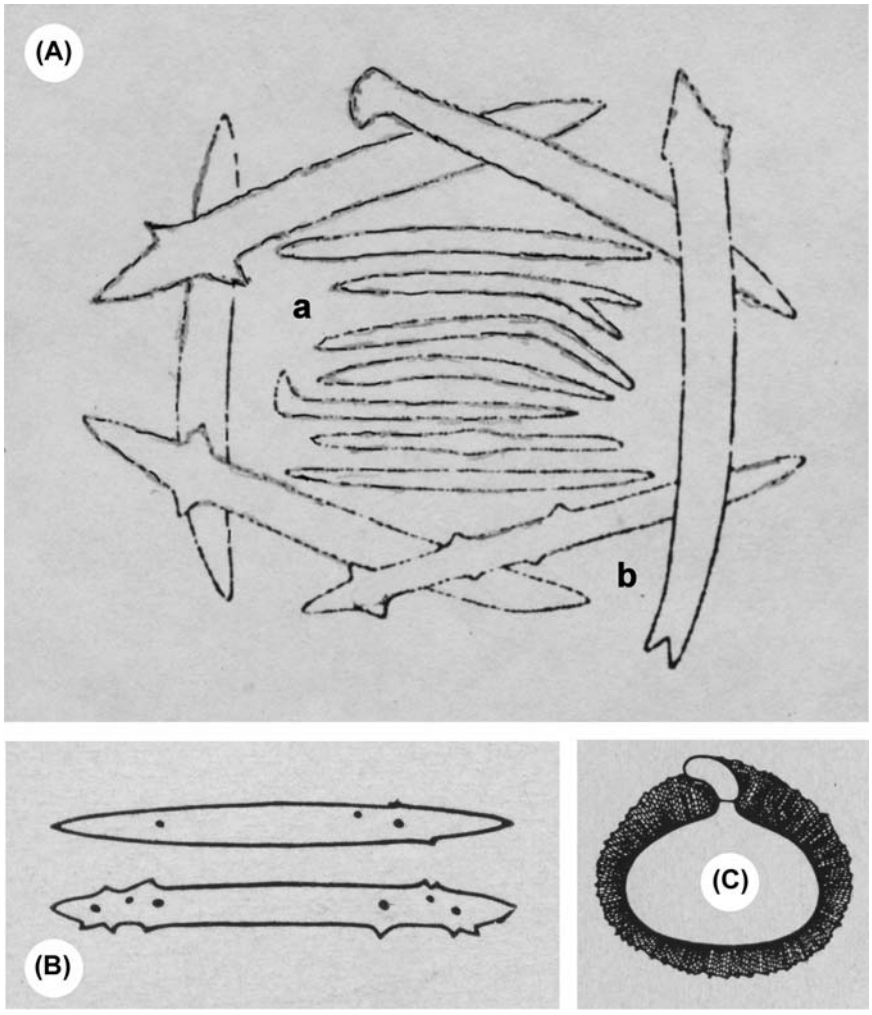


FIGURE 3.24 *Eunapius sinensis* (Annandale, 1910). (A) Pictorial representation of the spicular complement, not to scale. (Aa) Megascleres; (Ab) gemmuloscleres; (B) gemmuloscleres; (C) cross-section of a gemmule. *(A) Modified from Gee, 1927; (B and C) modified from Penney & Racek, 1968.*

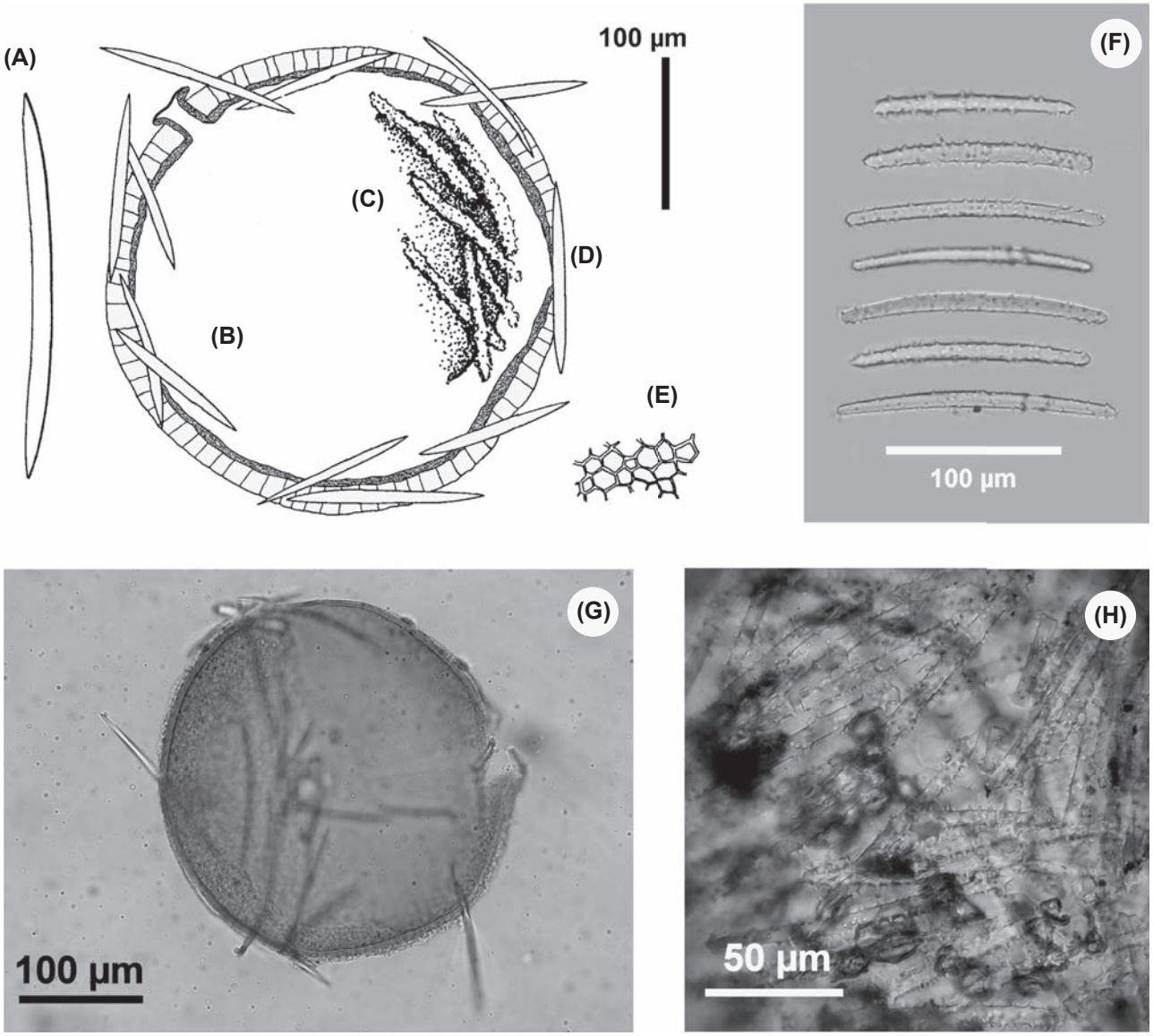


FIGURE 3.25 *Eunapius aetheriae* (Annandale, 1913). (A) Smooth oxea megasclere; (B) gemmule with foramen, pneumatic layer, and two types of gemmuloscleres; (C) acanthostrongyles (gemmuloscleres); (D) smooth oxea (gemmulosclere); (E) gemmular surface with polygonal ornamentation of spongin (outline of pneumatic layer chambers); (F) acanthostrongyles (gemmuloscleres); (G) gemmular theca outer layer of spongin with a few smooth oxeas; (H) gemmular inner layer with dense tangential acanthostrongyles (gemmuloscleres). *(A–E) Modified from Gugel, 1993; (F–H) modified from Manconi & Pronzato, 2009.*

Spongillida: Spongillidae: *Radiospongilla*: Species

1	Megascleres spiny oxeas; gemmuloscleres spiny strongyles radially oriented 2
1′	Megascleres oxeas entirely smooth (240–330 × 10–12 µm); gemmuloscleres spiny oxeas (72–110 × 2–4 m) with bent spines; gemmules 420–590 µm in diameter (Fig. 3.29) ..... *Radiospongilla cerebellata* (Bowerbank, 1863) [Japan. Pakistan. Widespread: Afrotropical, Australian, Oriental regions]
2(1)	Gemmuloscleres spiny strongyles; absence of abnormally short gemmuloscleres 3
2′	Skeleton spicules microspined (220–340 × 8–15 µm); gemmuloscleres large (65–160 × 5–8 µm), covered with a number of spines abnormally short also present (20–30 × 15 µm); gemmules 550–800 µm in diameter (Fig. 3.30) .... *Radiospongilla sendai* (Sasaki, 1936) [Japan. Korea]

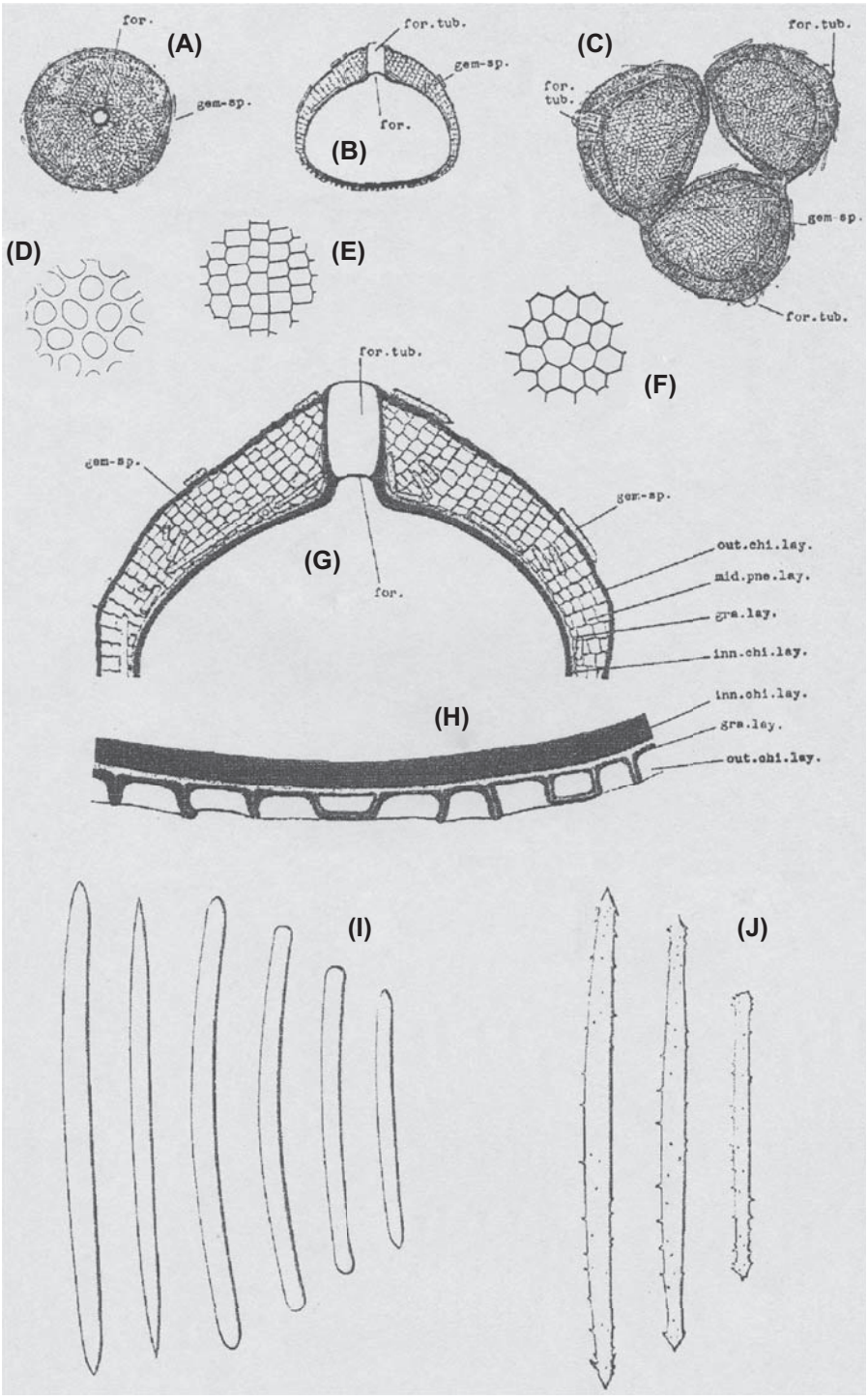


FIGURE 3.26 *Eunapius ryuensis* (Sasaki, 1970). (A) Gemmule with foramen; (B) gemmule (cross-section); (C) group of gemmules; (D–F) gemmular theca with polygonal outlines of pneumatic layer chambers; (G) magnification of the gemmular theca (cross-section); (H) outer layer of the gemmular theca; (I) megascleres; (J) spiny oxeas and strongyles (gemmuloscleres) (not to scale). *Modified from Sasaki, 1970.*

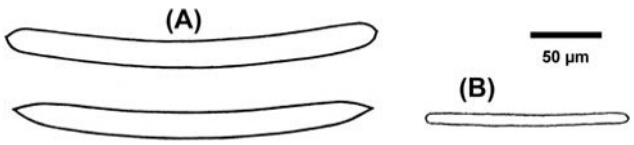


FIGURE 3.27 *Stratospongilla clementis* (Annandale, 1909). (A) Megascleres; (B) smooth strongyle (gemmulosclere). *Modified from Penney & Racek, 1968.*

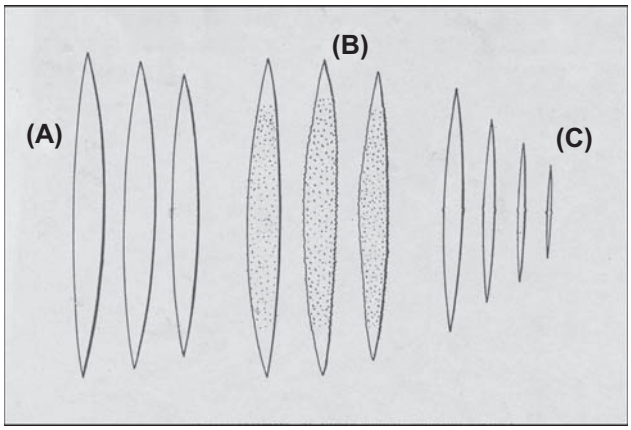


FIGURE 3.28 *Stratospongilla akanensis* (Sasaki, 1934). (A) Smooth oxeas megascleres; (B) spinyoxeas megascleres; (C) immature megascleres (not to scale). *Modified from Sasaki, 1934.*

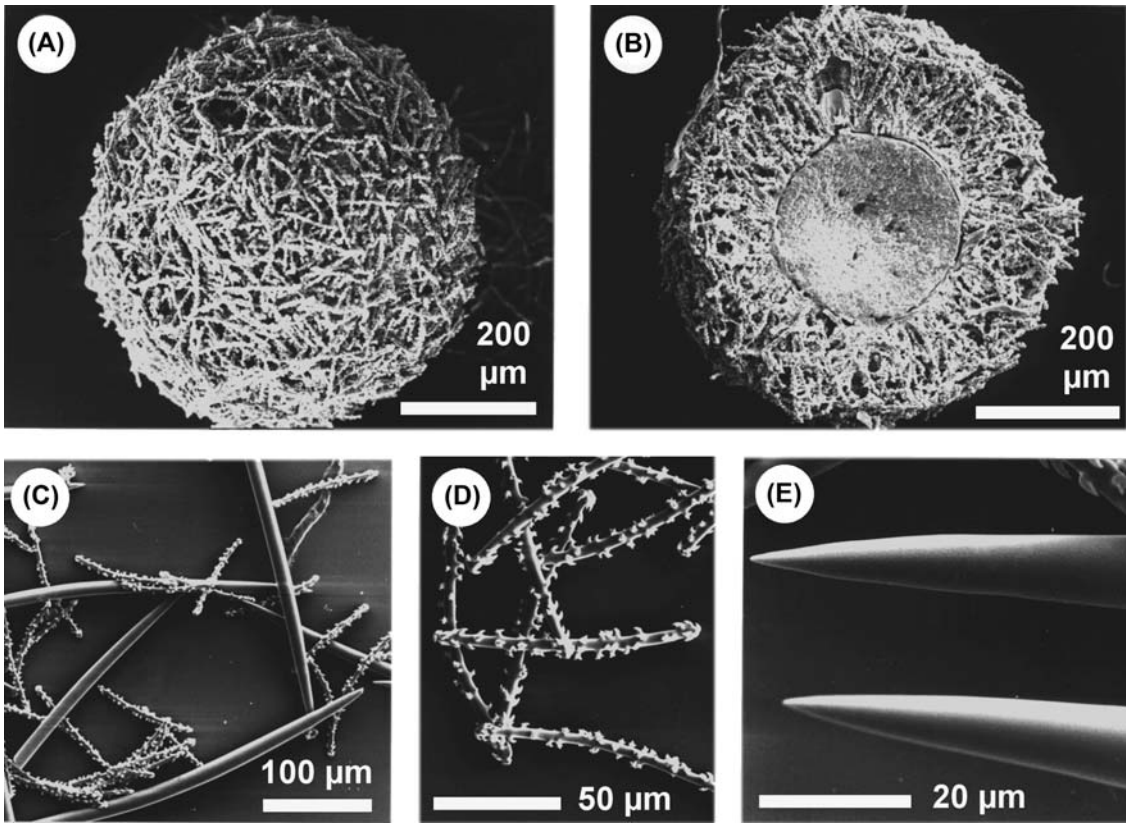


FIGURE 3.29 *Radiospongilla cerebellata* (Bowerbank, 1863). (A) Gemmule; (B) gemmule (cross-section); (C) spicular complement; (D) gemmuloscleres; (E) oxeas tips (megascleres). *Modified from Pronzato & Manconi, 2001.*

3(2) Megascleres microspiny oxeas <240 µm in length 4

3′ Megascleres oxeas scantly microspinose except at tips, > 230 µm (240–300 × 9–11 µm); gemmuloscleres spiny strongyles (60–75 × 3–5 µm) with small conical spines arranged in pseudorotule-like distal tips; gemmules 370–450 µm in diameter (Fig. 3.31) ..... *Radiospongilla crateriformis* (Potts, 1882)
[Japan. Widespread: Australia, Nearctic, Neotropical, Oriental regions]

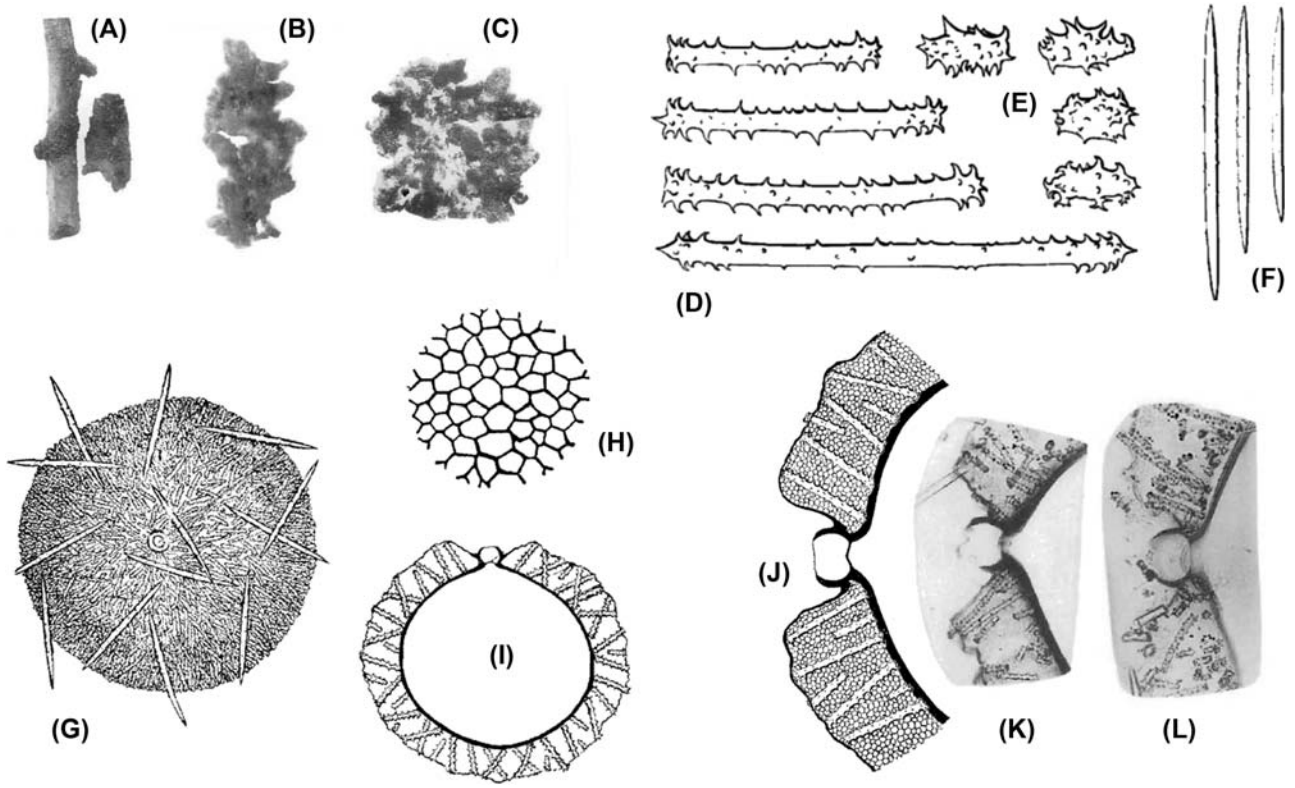


FIGURE 3.30 *Radiospongilla sendai* (Sasaki, 1936). (A–C) Growth forms; (D) gemmuloscleres; (E) small gemmuloscleres; (F) megascleres; (G) gemmule with foramen; (H) pneumatic layer (detail); (I) gemmule with foramen (cross-section); (J–L) cross-section of the foramen (not to scale). *Modified from Sasaki, 1936.*

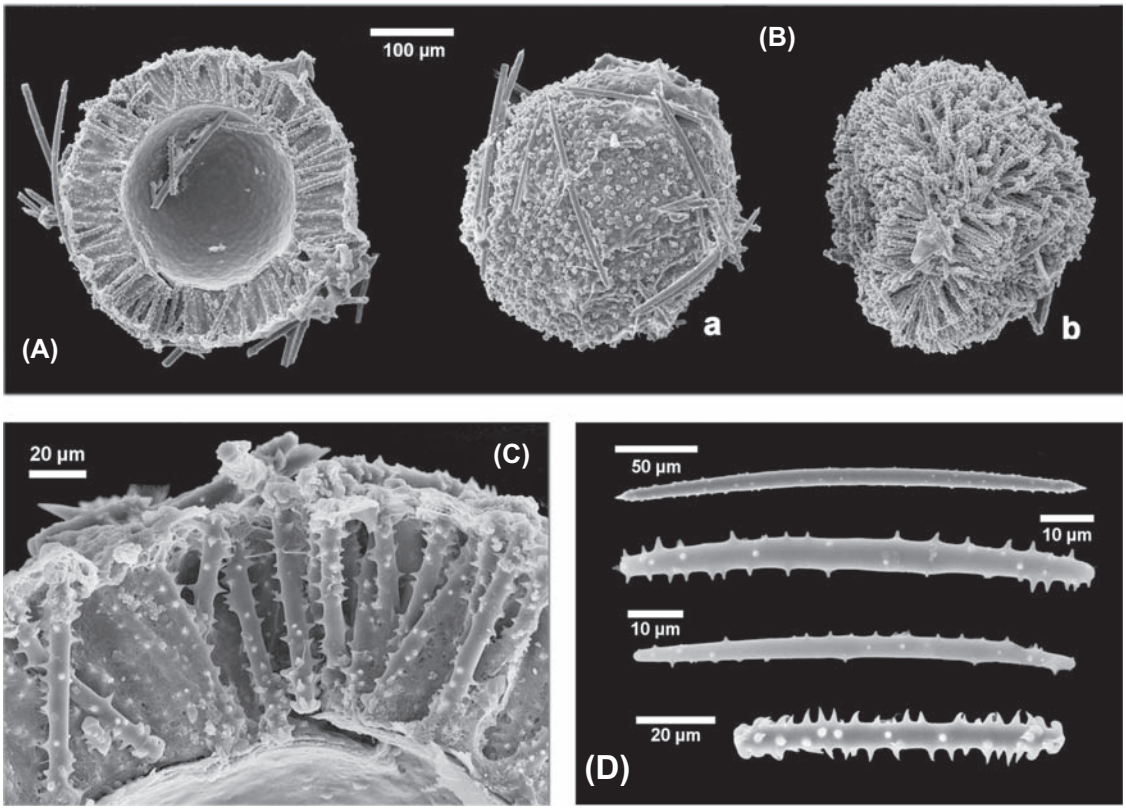


FIGURE 3.31 *Radiospongilla crateriformis* (Potts, 1882). (A) Gemmule (cross-section); (Ba) gemmule with the outer layer pierced by distal rotules of radial gemmuloscleres; (Bb) gemmule without outer layer; (C) gemmular theca (cross-section) with proximal rotules of radial gemmuloscleres adhering to the inner layer; pneumatic layer as thin scattered spongin fibers; (D) spicular complement. *Modified from Manconi & Pronzato, 2005.*

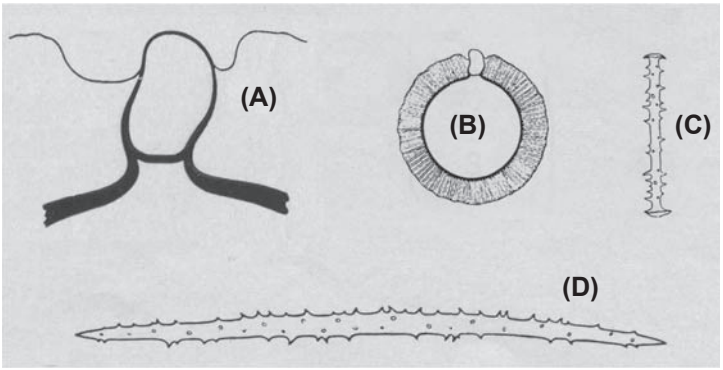


FIGURE 3.32 *Radiospongilla cantonensis* (Gee, 1929). (A) Gemmular foramen; (B) gemmule (cross-section); (C) gemmulosclere; (D) megasclere. *Modified from Penney & Racek, 1968.*

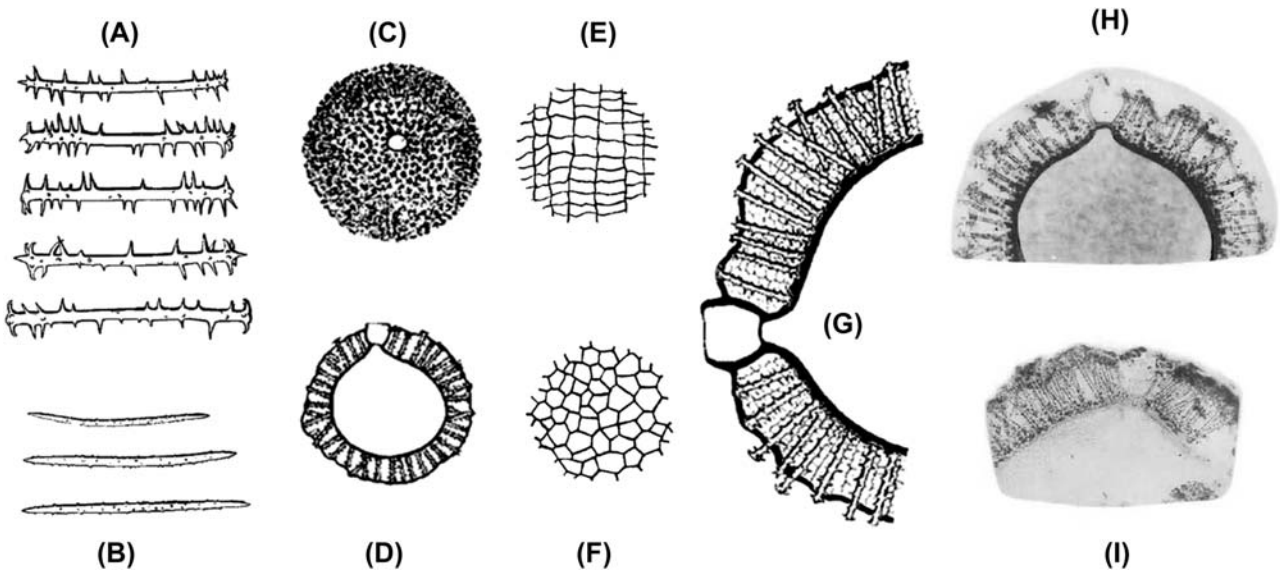


FIGURE 3.33 *Radiospongilla hozawai* (Sasaki, 1936). (A) Gemmuloscleres; (B) megascleres; (C) gemmule with the foramen; (D) gemmule cross-section through the foramen; (E–F) pneumatic layer cross- and tangential sections, respectively; (G–I) gemmular theca cross-section (not to scale). *Modified from Sasaki, 1936.*

4(3) Megascleres with oxeas scantly microspinose except at tips (180–230 × 8–11 μm); gemmuloscleres spiny oxeas (65–72 × 5 μm) with long, acute, bent spines arranged as small rotules at distal tips; gemmules 365–410 μm in diameter (Fig. 3.32) ..... *Radiospongilla cantonensis* (Gee, 1929) [China]

4′ Skeleton spicules relatively small, microspiny (160–230 × 5–8 μm); gemmuloscleres thin (55–72 × 3–4 μm) covered by straight or bent spines; gemmules 310–380 μm in diameter (Fig. 3.33) ..... *Radiospongilla hozawai* (Sasaki, 1936) [Incompletely described species. Japan]

Spongillida: Spongillidae: *Trochospongilla*: Species

1 Megascleres smooth 2

1′ Megascleres spiny, 170–235 μm long; gemmuloscleres with short shaft (c. 10 μm) (Fig. 3.34) ..... *Trochospongilla horrida* (Weltner, 1893) [Holarctic]

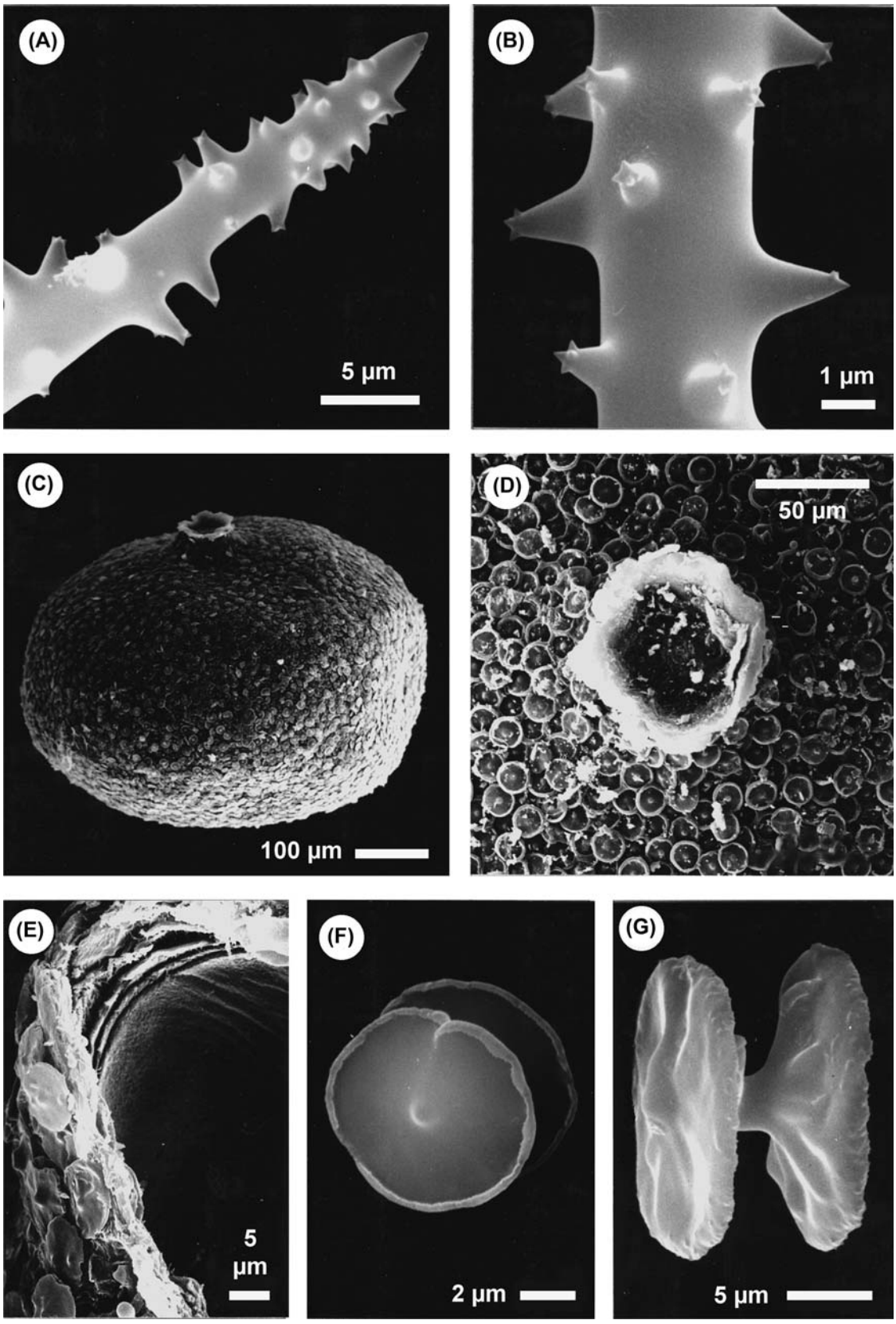


FIGURE 3.34 *Trochospongilla horrida* Weltner, 1893. (A) Megasclere spiny tip; (B) spines of megascleres shaft; (C) gemmule; (D) foramen; (E) gemmular theca cross-section; (F—G) gemmuloscleres. *Modified from Pronzato & Manconi, 2001.*

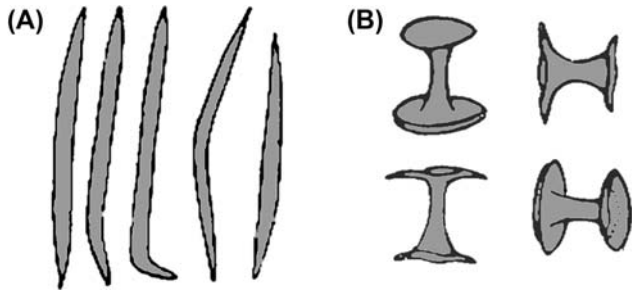


FIGURE 3.35 *Trochospongilla singpuensis* Cheng, 1991. (A) Smooth oxeas (megascleres); (B) birotules (gemmuloscleres). *Modified from Cheng, 1991.*

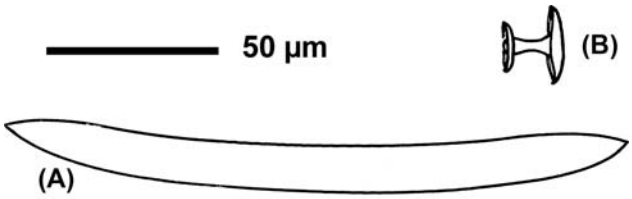


FIGURE 3.36 *Trochospongilla latouchiana* Annandale, 1907. (A) Megasclere smooth oxea; (B) gemmulosclere birotule. *Modified from Penney & Racek, 1968.*

2(1) Megascleres smooth oxeas 144−256 µm long, with evident angles, often at tips; gemmuloscleres with a slender (2−4 µm) shaft (Fig. 3.35) ..... *Trochospongilla singpuensis* Cheng, 1991
[Incompletely described species. China; Hebei]

2′ Megascleres smooth oxeas 220−310 µm long, almost straight; gemmuloscleres minute, slender, long shaft (13−17 µm) (Fig. 3.36) ..... *Trochospongilla latouchiana* Annandale, 1907
[China. Afrotropical, Australian, and Oriental regions]

Spongillida: Spongillidae: *Corvospongilla*: Species

1 Megascleres oxeas to strongyles, smooth to spiny 2

1′ Megascleres oxeas to strongyles, smooth to spiny (two length classes: 125−150 µm and 220−225 µm); microscleres pseudobirotules with bent hooks at tips; gemmuloscleres stout, spiny strongyles (Fig. 3.37) ..... *Corvospongilla loricata* (Weltner, 1895)
[Egypt]

2(1) Megascleres smooth oxeas to strongyles (210−290 µm); microscleres pseudobirotules with bent hooks at tips; gemmuloscleres stout, spiny oxeas to strongyles (Fig. 3.38) ..... *Corvospongilla mesopotamica* Manconi & Pronzato, 2004
[Iraq]

2′ Megascleres spiny strongyles (120−150 µm); microscleres pseudobirotules with bent hooks at tips; gemmuloscleres spiny strongyles (Fig. 3.39) ..... *Corvospongilla scabrispiculis* Annandale, 1913
[Egypt]

Spongillida: Spongillidae: *Ephydatia*: Species

1 Spiny megascleres 2

1′ Megascleres entirely smooth to microspiny 3

2(1) Gemmuloscleres with smooth short shaft (12−20 × 4−6 µm), rotules 20−25 µm in diameter (Fig. 3.40) ..... *Ephydatia muelleri* (Lieberkühn, 1856)
[Holarctic]

2′ Gemmuloscleres with spiny long shaft (38−65 × 6−8 µm); rotules 23−28 µm in diameter (Fig. 3.41) ..... *Ephydatia fortis* Weltner, 1895
[Japan. Oriental Region]

3(1) Megascleres microspiny 4

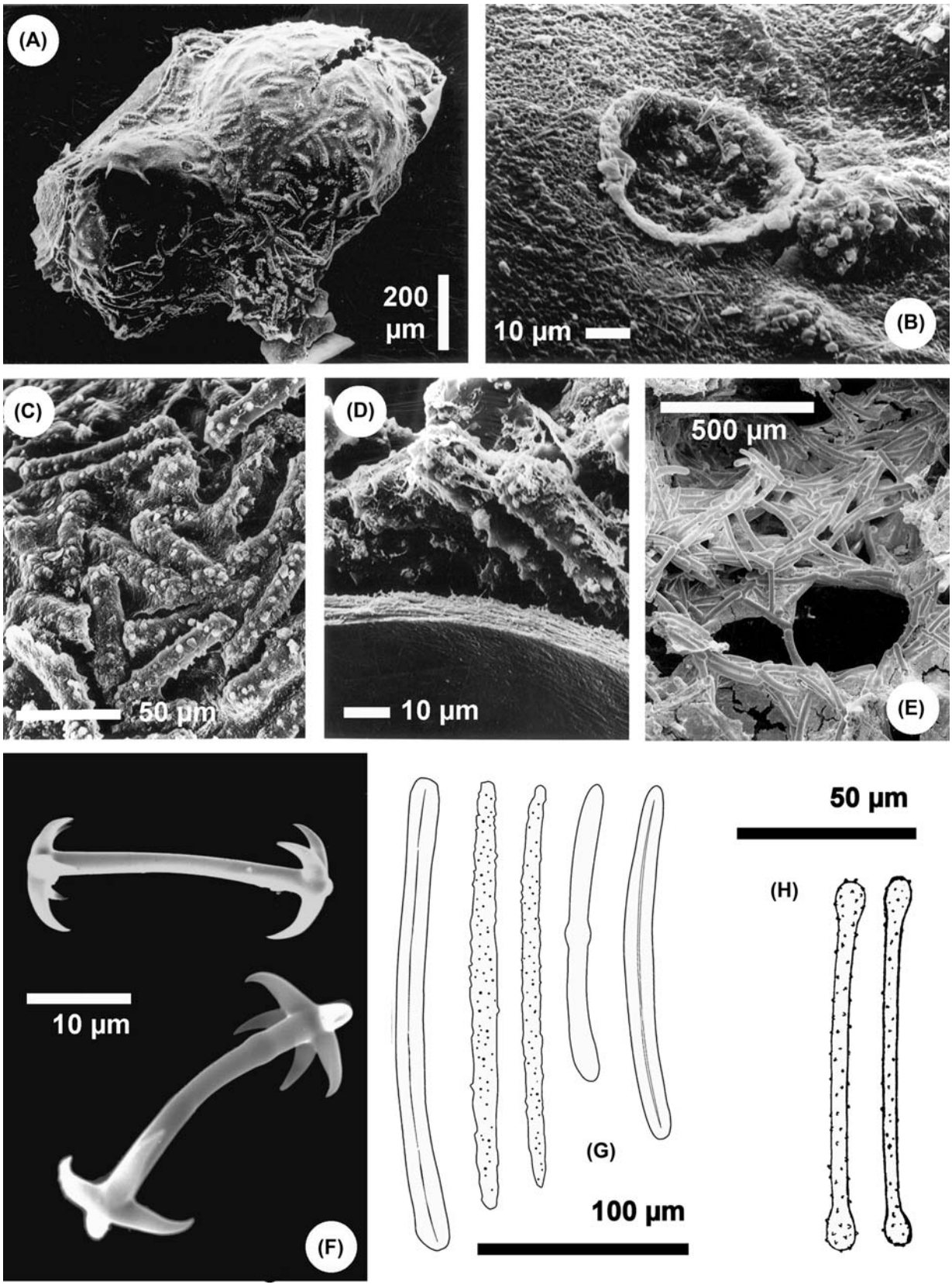


FIGURE 3.37 *Corvospongilla loricata* (Weltner, 1895). (A) Gemmular cage enveloping two sessile gemmules; (B) foramen; (C) gemmular surface with gemmuloscleres; (D) gemmular theca (cross-section); (E) skeletal network; (F) micropseudobirotules (microscleres); (G–H) megascleres. *(A–F) Modified from Manconi & Pronzato, 2002; (G–H) modified from Manconi & Pronzato, 2004.*

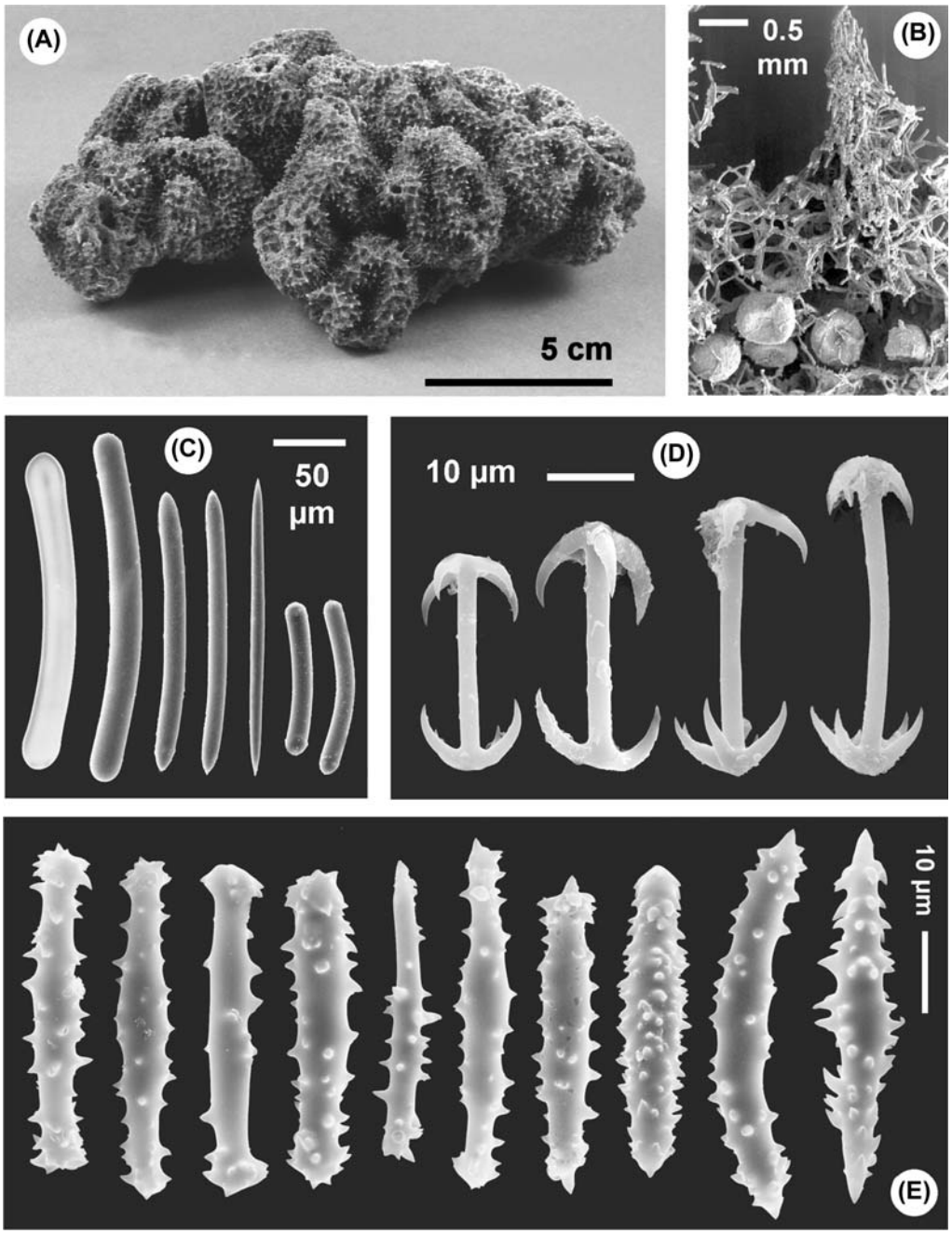


FIGURE 3.38 *Corvospongilla mesopotamica* Manconi & Pronzato, 2004. (A) Holotype, Museo Civico di Storia Naturale, Genova, MSNG51766; (B) ectosomal skeleton (cross-section, lateral view) with a conule and a group of gemmules in the choanosomal network; (C) strongyles and oxeas (skeletal megascleres) and short strongyles of the gemmular cage (right); (D) micropseudobirotules (microscleres) armed with recurved hooks; (E) spiny strongyles and oxeas (gemmuloscleres); (F–J) sessile gemmules; (F) gemmular cage; (G) cage surface as a dense mosaic-like layer of spiny to smooth strongyles; (H) gemmular theca within the cage (cross-section); (I) gemmular cage and theca (cross-section); (J) gemmular theca of compact spongin with spiny strongyles and sublayered inner layer (cross-section); (K–O) free gemmules; (K) gemmular theca (surface); (L) gemmular theca (cross-section); (M) foramen (detail); (N) pneumatic layer with embedded spiny strongyles/oxeas toward the inner layer; (O) gemmular outer layer with rare spiny oxeas piercing the surface. *Modified from Manconi & Pronzato, 2004.*

3′	Megascleres entirely smooth	5
4(3)	Gemmuloscleres with spiny shaft (30–43 × 5–6 µm); rotules diameter 23–27 µm (Fig. 3.42)	*Ephydatia syriaca* Topsent, 1910 [Syria]
4′	Gemmuloscleres smooth/spiny shaft (20–30 × 3–4 µm); rotules 18–21 µm in diameter (Fig. 3.43)	*Ephydatia fluviatilis* (Linnaeus, 1759) [Cosmopolitan]

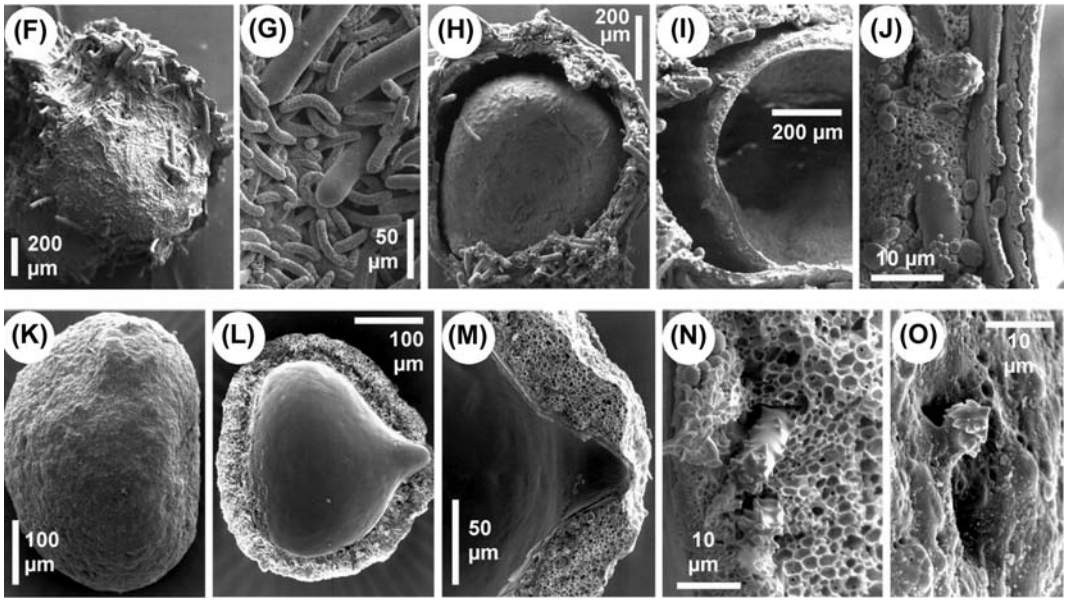


FIGURE 3.38 Cont'd

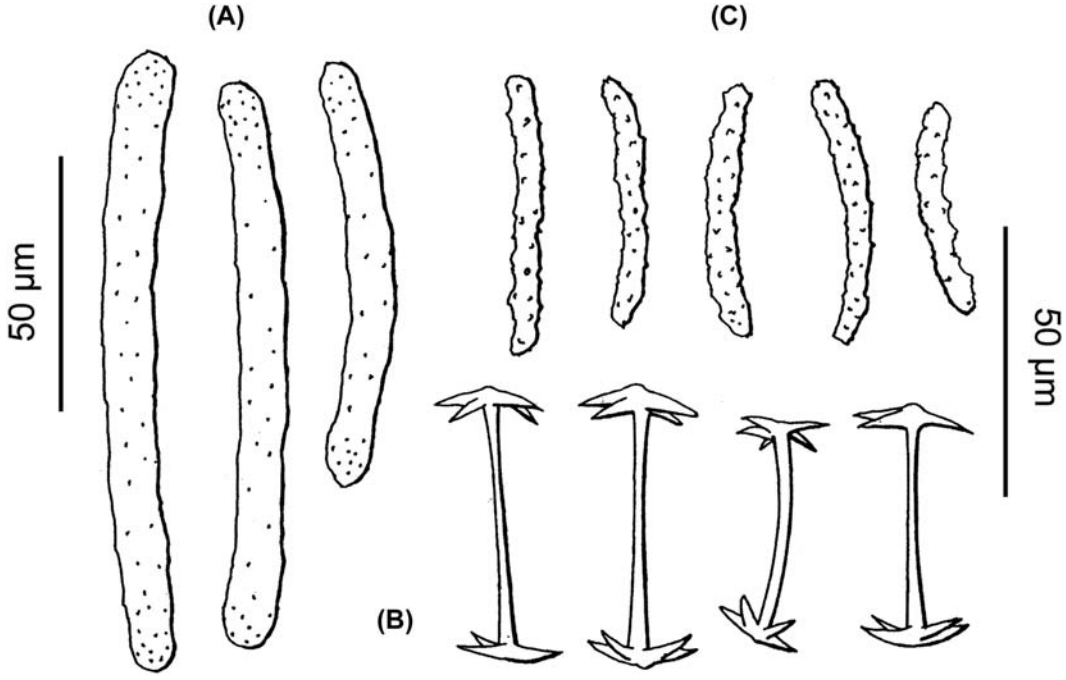


FIGURE 3.39 *Corvospongilla scabrispiculis* Annandale, 1913. (A) Strongyles (megascleres); (B) micropseudobirotules (microscleres); (C) strongyles (gemmuloscleres). *Modified from Gugel, 1993.*

5(3) Gemmuloscleres long smooth occasionally spiny shaft (28–33 × 5–6 µm); rotules 25–29 µm in diameter (Fig. 3.44) ..... *Ephydatia meyeni* (Carter, 1849)
[China. Oriental Region]

5′ Gemmuloscleres short smooth shaft (12–15 × 4–6 µm); rotules 16–22 µm in diameter (Fig. 3.45) ..... *Ephydatia japonica* (Hilgendorf, 1882)
[China. Japan]

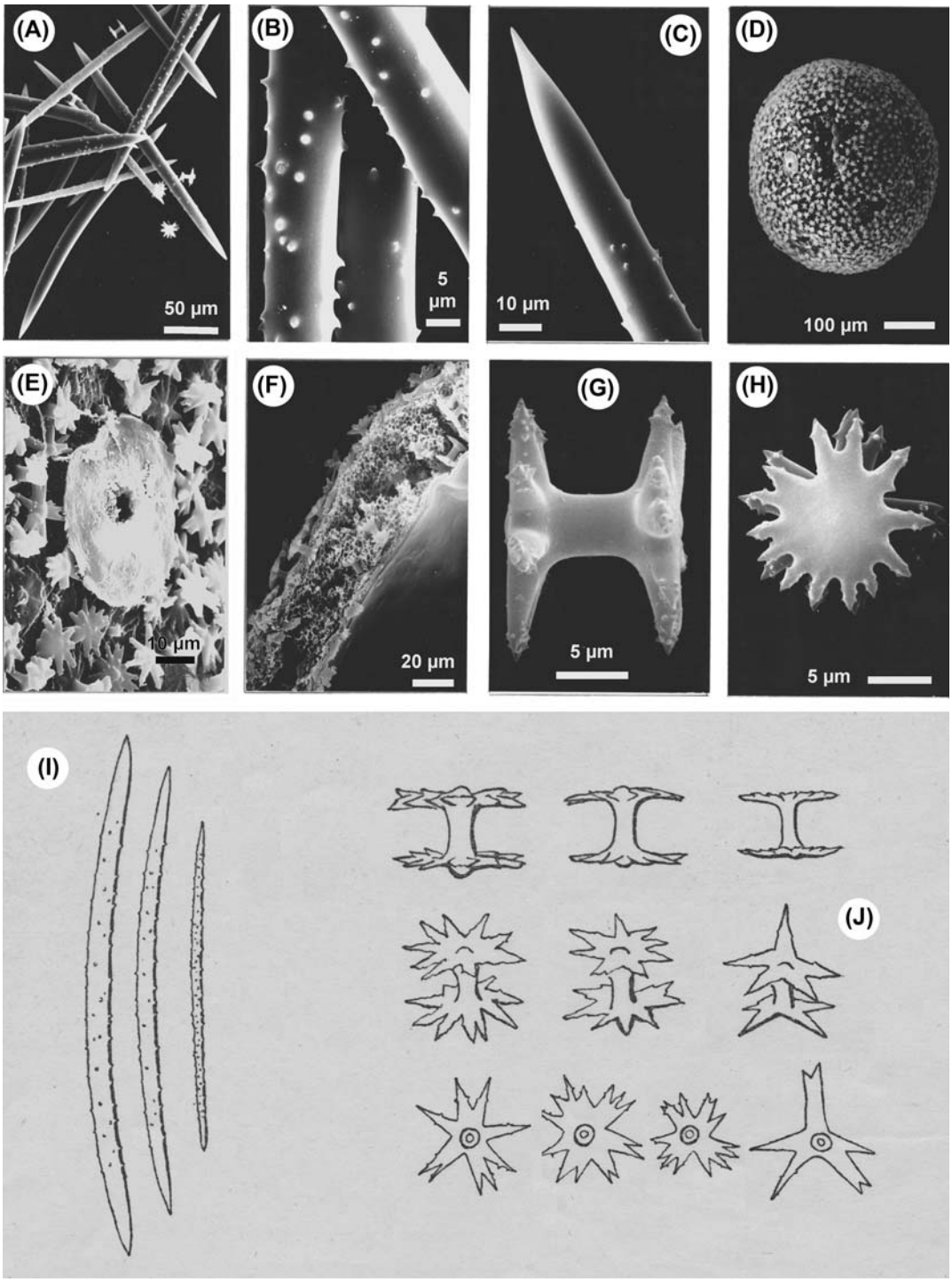


FIGURE 3.40 *Ephydatia muelleri* (Lieberkühn, 1856). (A) Spiny oxeas (megascleres) and birotules (gemmuloscleres); (B) megasclere shafts; (C) megasclere tip; (D) gemmule; (E) foramen; (F) trilayered pneumatic theca; (G) birotule (gemmulosclere); (H) rotule of a gemmulosclere; (I) oxeas (megascleres); (J) birotules (gemmuloscleres). *(A–H) Modified from Manconi & Pronzato, 2004; (I–J) modified from Sasaki, 1939.*



FIGURE 3.41 *Ephydatia fortis* Weltner, 1895. (A) Birotule (gemmulosclere, lateral view); (B) rotule (top view); (C) rotule (lateral view). *Modified from Penney & Racek, 1968.*

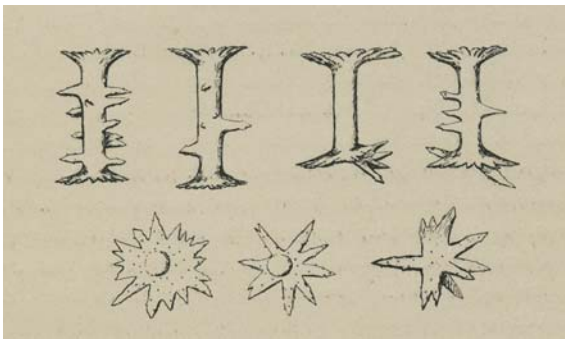


FIGURE 3.42 *Ephydatia syriaca* Topsent, 1910. Birotules (gemmuloscleres, lateral and top view). *Modified from Topsent, 1910.*

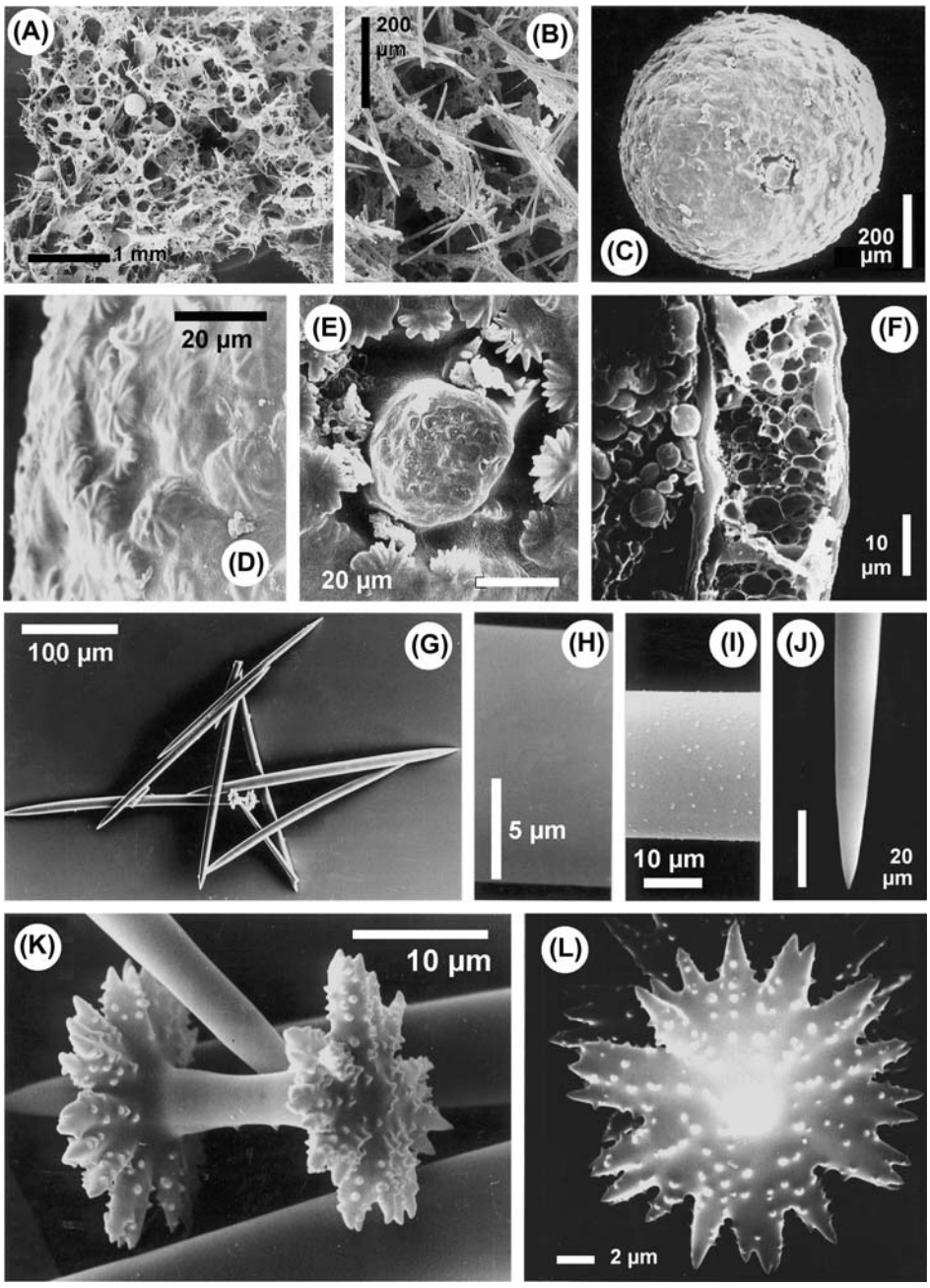


FIGURE 3.43 *Ephydatia fluviatilis* (Linnaeus, 1759). (A–B) Skeletal network; (C) gemmule; (D) gemmular surface; (E) foramen; (F) trilayered theca (multilayered inner layer, left); (G) spicular complement (one gemmulosclere and megascleres); (H) oxea with smooth shaft; (I) oxea shaft with granules/tubercles; (J) oxea tip; (K–L) birotules (gemmuloscleres). *(A–E, G–I, and K) Modified from Manconi & Pronzato, 2002; (F, J, and L) modified from Pronzato & Manconi, 2001.*

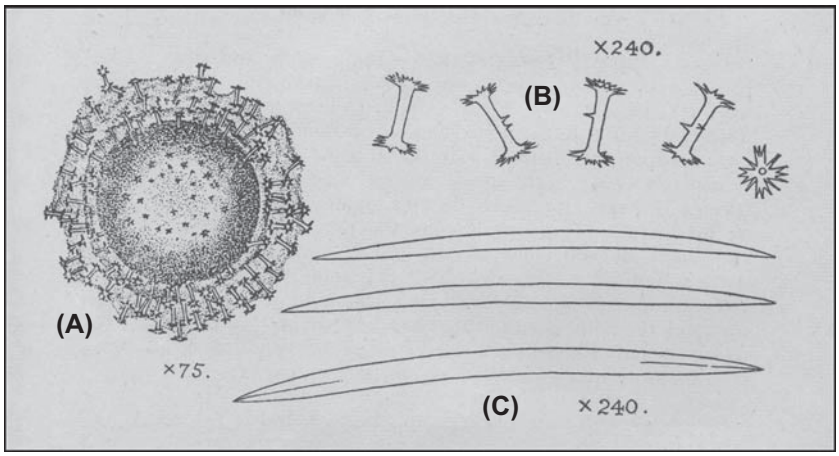


FIGURE 3.44 *Ephydatia meyeni* (Carter, 1849). (A) Gemmule; (B) birotules (gemmuloscleres); (C) oxeas (megascleres). *Modified from Annandale, 1911.*

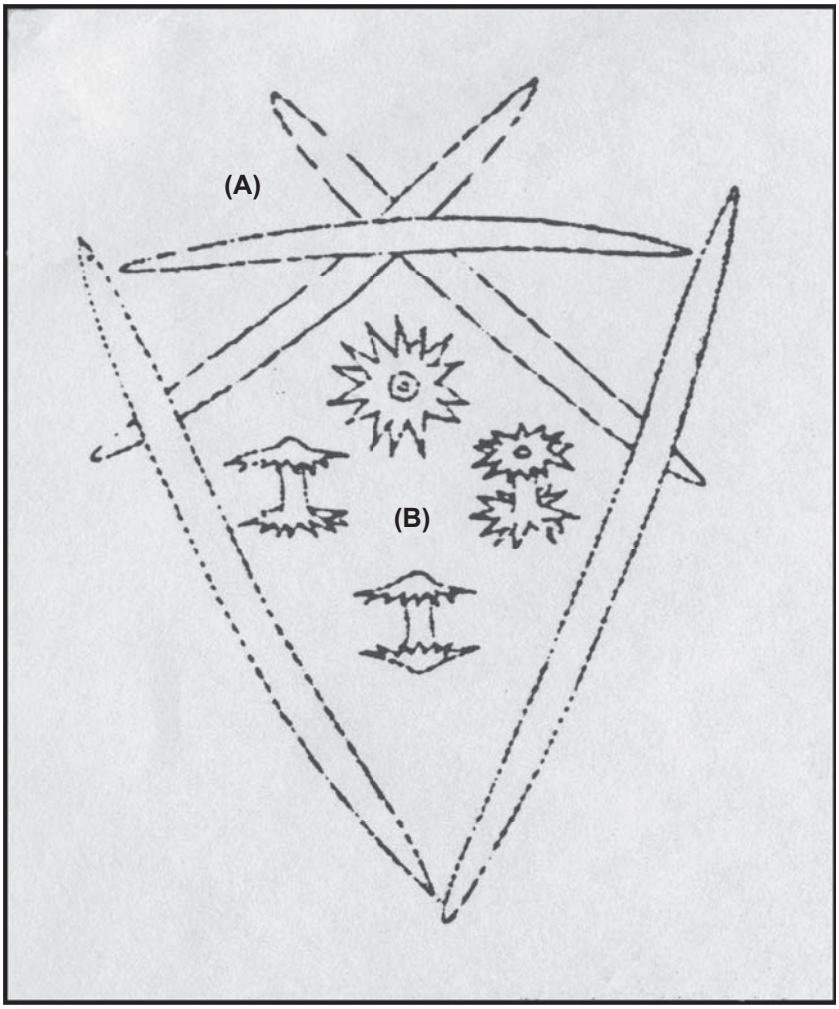


FIGURE 3.45 *Ephydatia japonica* (Hilgendorf, 1882). Pictorial representation of the spicular complement (not to scale). (A) Oxeas (megascleres); (B) birotules (gemmuloscleres). *Modified from Gee, 1927.*

Spongillida: Spongillidae: *Heteromeyenia*: Species

1 Megascleres oxeas scantly microspiny (255–315 µm); microscleres heavy spiny (asterose) (75–85 µm); gemmuloscleres birotules (two length classes: 50–60/80–85 µm); gemmular foramen tubular without terminal cirri filaments (Fig. 3.46) ..... *Heteromeyenia baileyi* (Bowerbank, 1863)
[Holarctic. Neotropical]

1′ Megascleres oxeas sparcely microspiny (180–310 µm); microscleres densely spiny (hooks) (78–86 µm); gemmuloscleres birotules (two length classes: 58–65/75–88 µm); gemmular foramen tubular with terminal crown like rim (Fig. 3.47) ..... *Heteromeyenia stepanowi* (Dybowski, 1884)
[Palaearctic. Australian and Neotropical regions]

Spongillida: Lubomirskiidae: Genera

1 Growth form massive (globular) to encrusting with digitiform outgrowths; consistency firm to hard; surface smooth 2

1′ Growth form encrusting to massive, branching; consistency soft; densely conulose, variably long conules ..... ***Rezinkovia***
[Lake Baikal]

2(1) Megascleres typically strongyles variably spiny 3

2′ Megascleres typically spiny oxeas ..... ***Lubomirskia*** **[p. 78]**

3(2) Megascleres typically smooth/spiny, stout, bent strongyles with spines in rosettes, rare spiny oxeas ..... ***Swartschewskia*** **[p. 78]**

3′ Megascleres typically smooth strongyles with spiny tips; spiny strongyles and/or smooth/spiny oxeas also present ..... ***Baikalospongia*** **[p. 84]**

Spongillida: Lubomirskiidae: *Rezinkovia*: Species

Two species endemic to Lake Baikal.

1 Conulose, dense, long conules; oxeas from stout to slender with spiny tips (Fig. 3.48) ..... *Rezinkovia echinata* Efremova, 2004

1′ Conulose, dense, short conules; oxeas stout, smooth (Fig. 3.49) ..... *Rezinkovia arbuscula* Efremova, 2004

Spongillida: Lubomirskiidae: *Lubomirskia*: Species

Endemic to Lake Baikal.

1 Massive to encrusting; smooth to variously spiny oxeas 2

1′ Digitate to arborescent up to >30–50 cm in height; spiny oxeas to strongyles (Fig. 3.50) ..... *Lubomirskia baikalensis* (Pallas, 1776)

2(1) Oxeas smooth to spiny particularly or only at tips 3

2′ Encrusting; regularly spiny oxeas (Fig. 3.51) ..... *Lubomirskia incrustans* Efremova, 2004

3(2) Oxeas entirely smooth to spiny (Fig. 3.52) ..... *Lubomirskia fusifera* Soukatschoff, 1896

3′ Oxeas smooth spiny at tips (Fig. 3.53) ..... *Lubomirskia abietina* Swartschewski, 1902

Spongillida: Lubomirskiidae: *Swartschewskia*: Species

Two species endemic to Lake Baikal.

1 Massive, rounded, bent strongyles; rare oxeas regularly spiny (Fig. 3.54) ..... *Swartschewskia papyracea* Dybowski, 1880

1′ Massive, irregular; bent smooth strongyles (Fig. 3.55) ..... *Swartschewskia irregularis* (Swartschewski, 1902)
[Incompletely described]

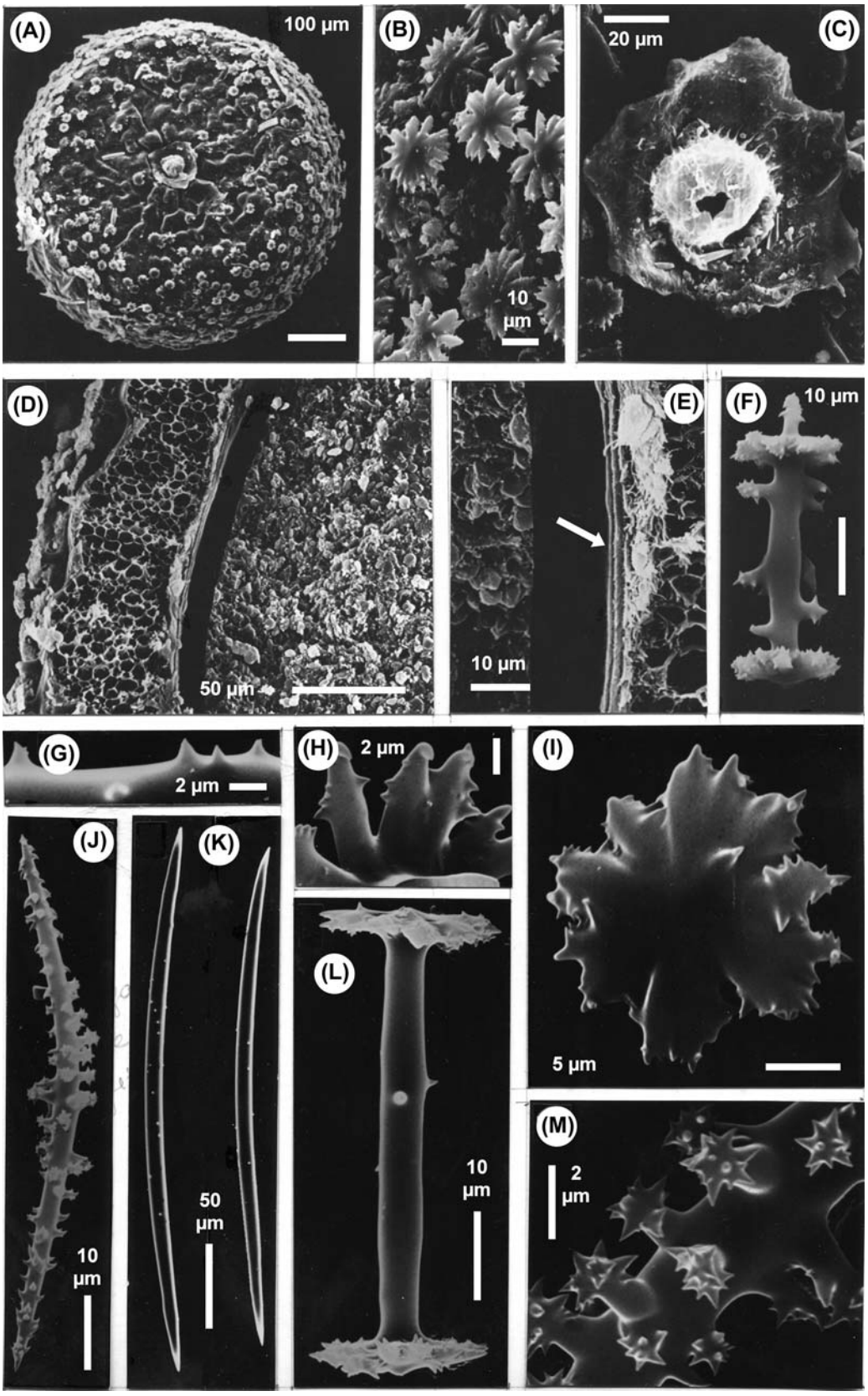


FIGURE 3.46 *Heteromeyenia baileyi* (Bowerbank, 1863). (A) Gemmule; (B) gemmular surface (close up); (C) foramen with foraminal tube; (D) trilayered theca; (E) gemmular theca with multilayered inner layer (arrow) of compact spongin; (F) short birotule (gemmulosclere); (G) oxea surface (megasclere); (H) rotule (inner view); (I) rotule (outer view); (J) spiny bent oxea (microsclere); (K) microspiny oxeas (megascleres); (L) long birotule gemmulosclere; (M) microsclere surface. *Modified from Pronzato & Manconi, 2001.*

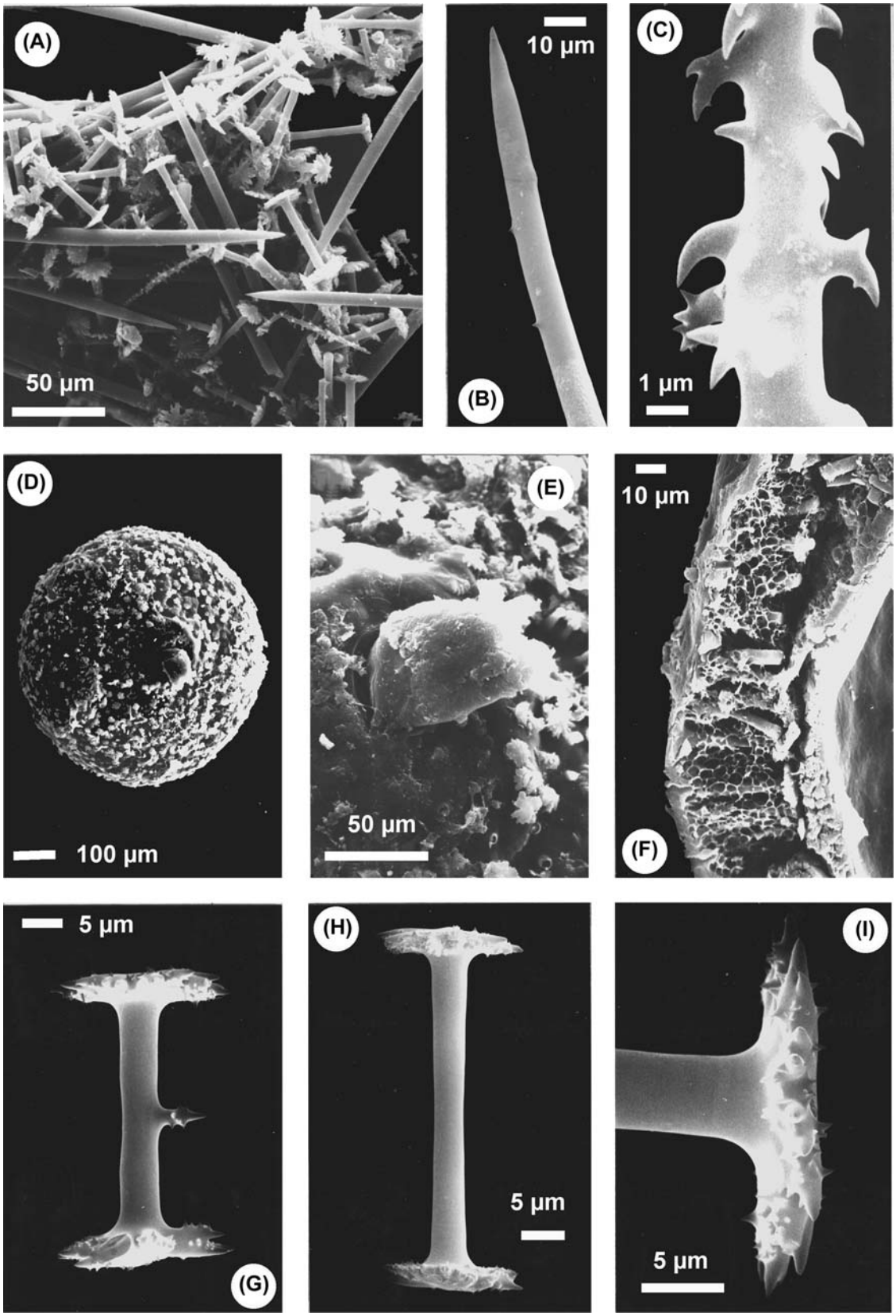


FIGURE 3.47 *Heteromeyenia stepanowi* (Dybowski, 1884). (A) Spicular complement of smooth oxeas (megascleres), spiny oxeas (microscleres), and two types of birotules (gemmuloscleres); (B) megasclere tip; (C) microsclere shaft; (D) gemmule; (E) foramen; (F) trilayered gemmular theca with pneuma; (G–H) two types of birotules (gemmuloscleres) with diverging shaft length; (I) magnification of a rotule (gemmulosclere). *Modified from Pronzato & Manconi, 2001.*

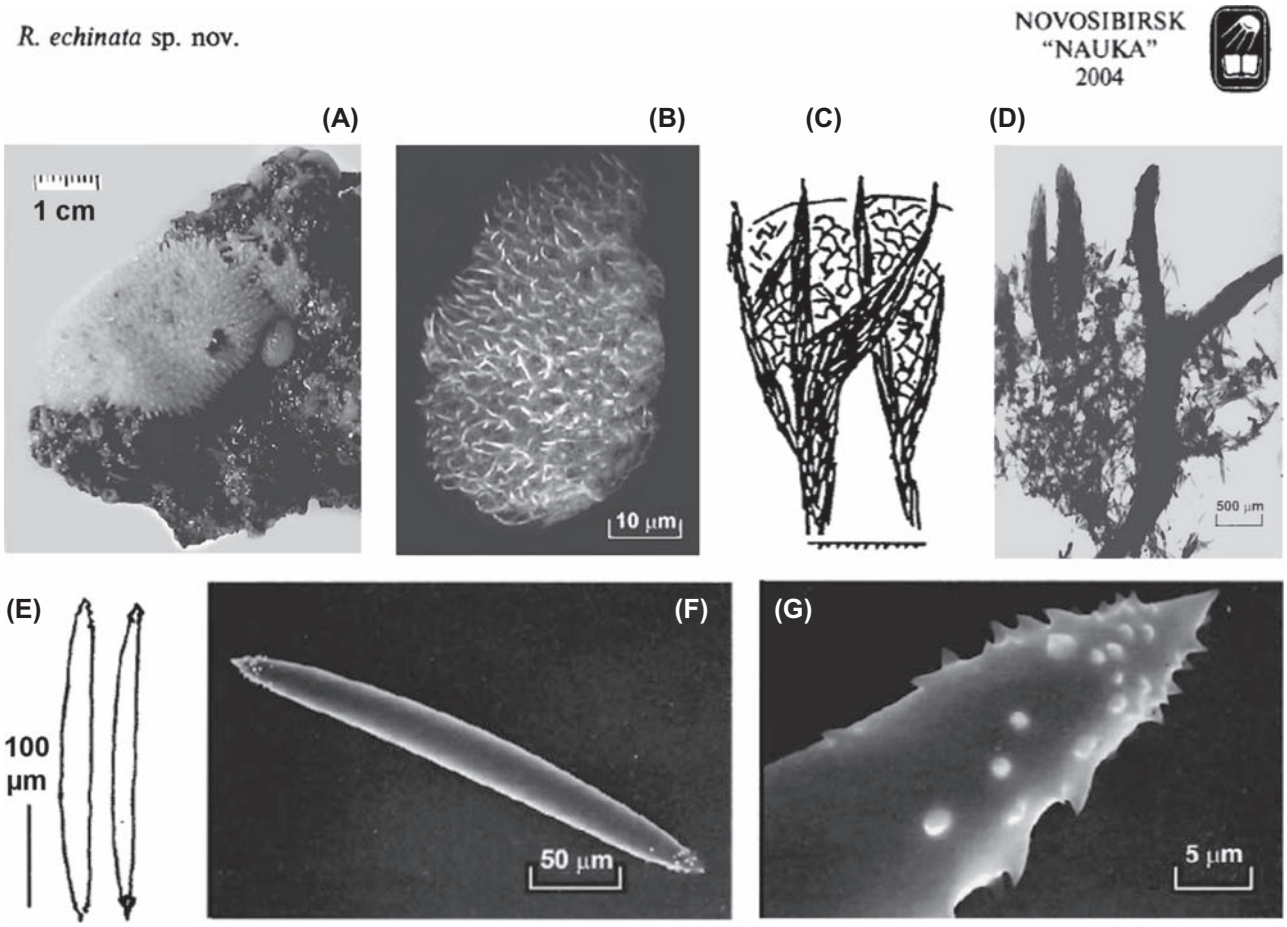


FIGURE 3.48 *Rezinkovia echinata* Efremova, 2004. (A) Specimen with conulose surface; (B) conules (close up); (C–D) skeletal architecture (cross-section); (E–G) spicular complement. *Modified from Efremova, 2004.*

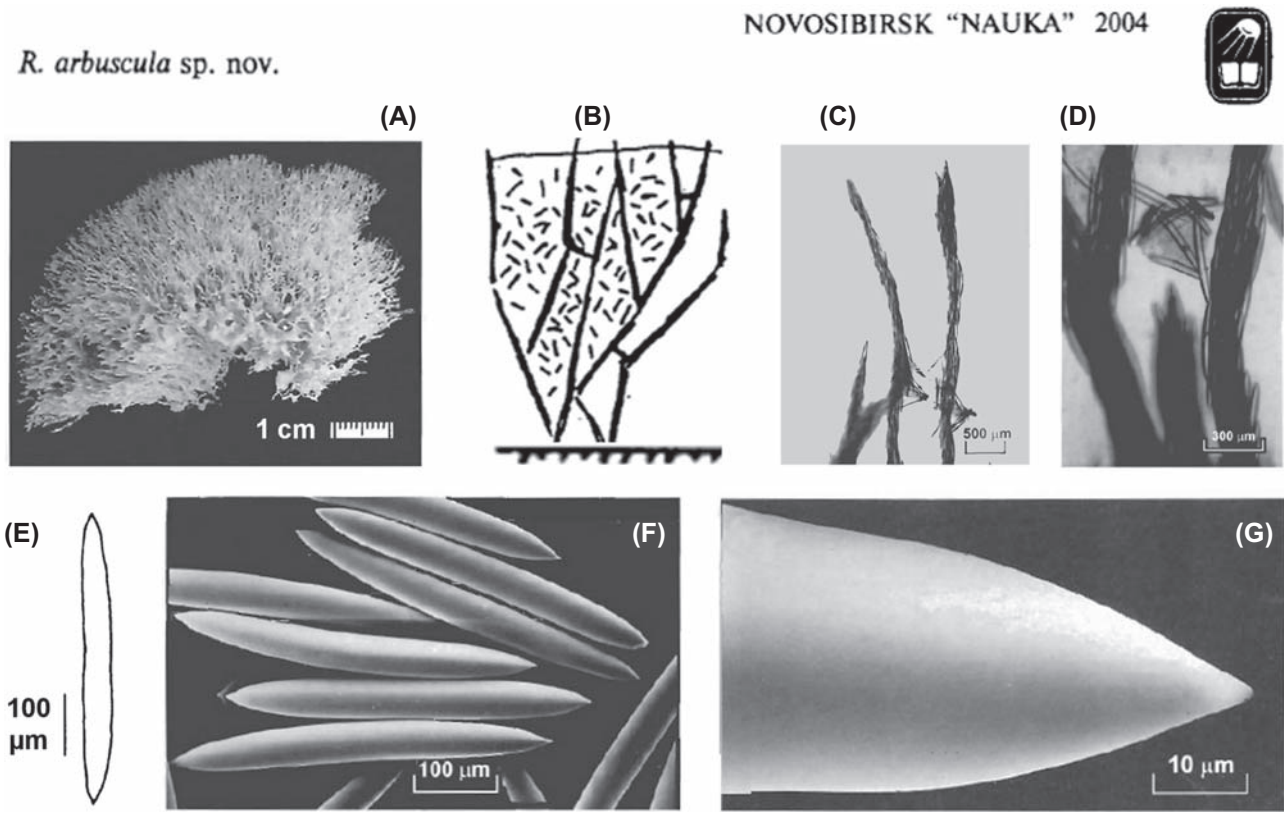


FIGURE 3.49 *Rezinkovia arbuscula* Efremova, 2004. (A) Specimen fragment; (B–D) skeletal architecture (cross-section); (E–G) spicular complement. *Modified from Efremova, 2004.*

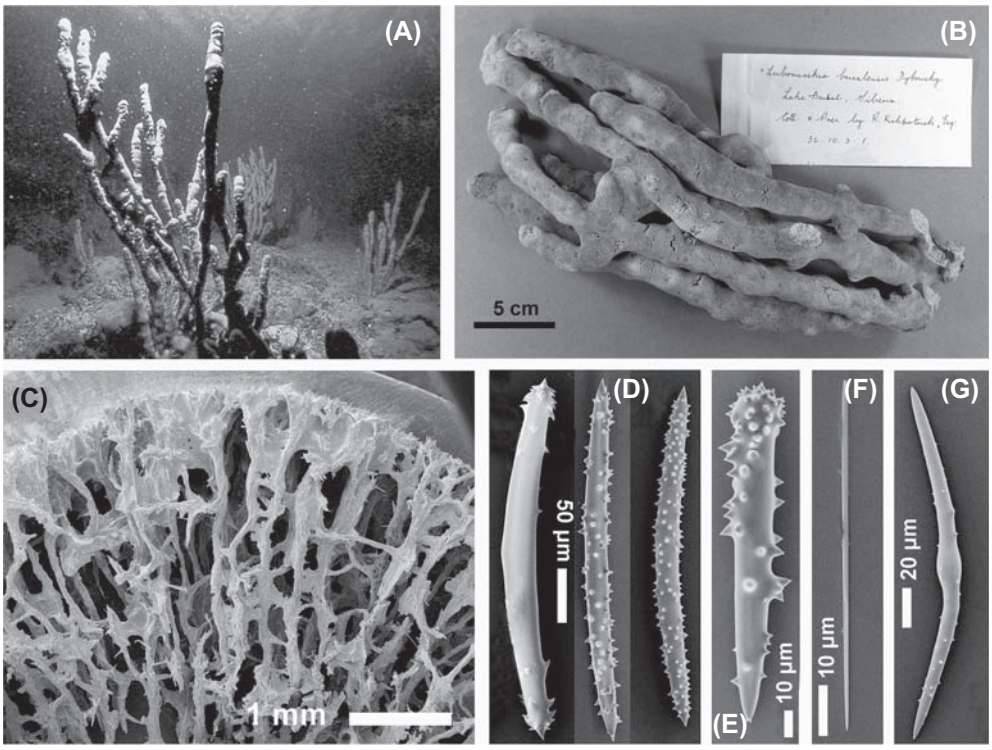


FIGURE 3.50 *Lubomirskia baikalensis* (Pallas, 1776). (A) Living specimen in its habitat; (B) large dry fragment; (C) skeletal architecture; (D–G) spicular complement. *Modified from Manconi & Pronzato, 2002.*

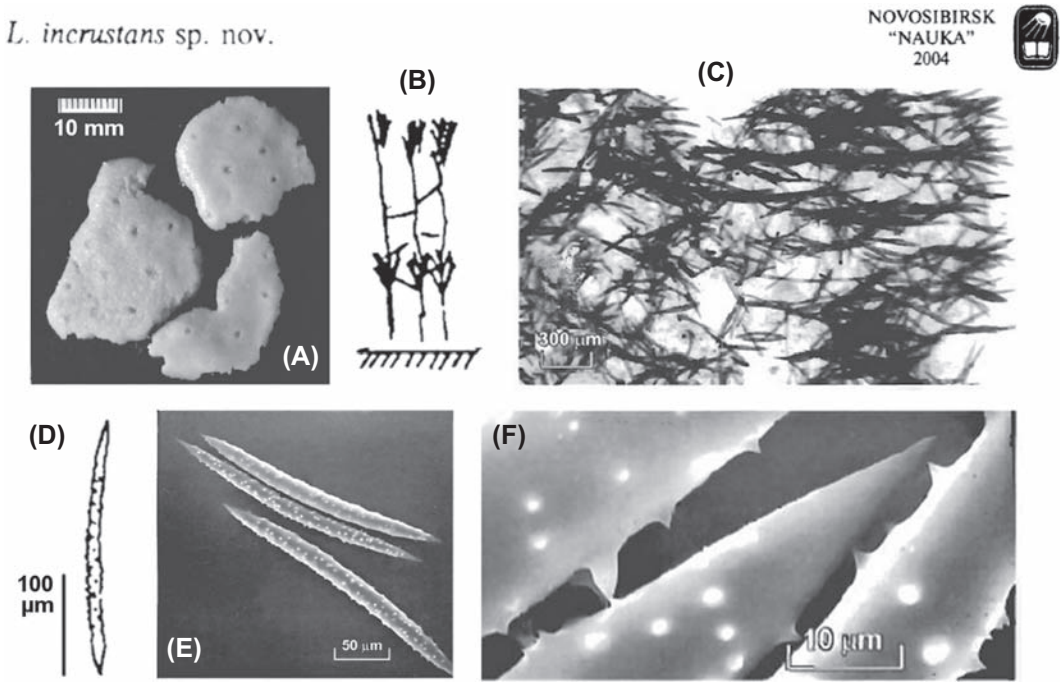


FIGURE 3.51 *Lubomirskia incrustans* Efremova, 2004. (A) Encrusting specimen (fragments); (B–C) skeletal architecture (cross-section); (D–F) spicular complement. *Modified from Efremova, 2004.*

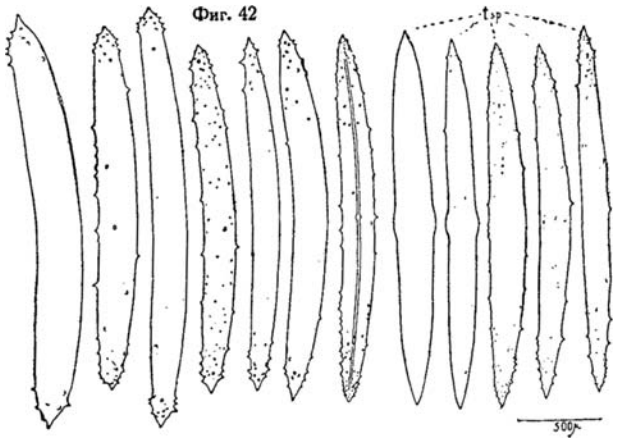


FIGURE 3.52 *Lubomirskia fusifera* Soukatschoff, 1896. Spicular complement. *Modified from Rezvoi, 1927.*

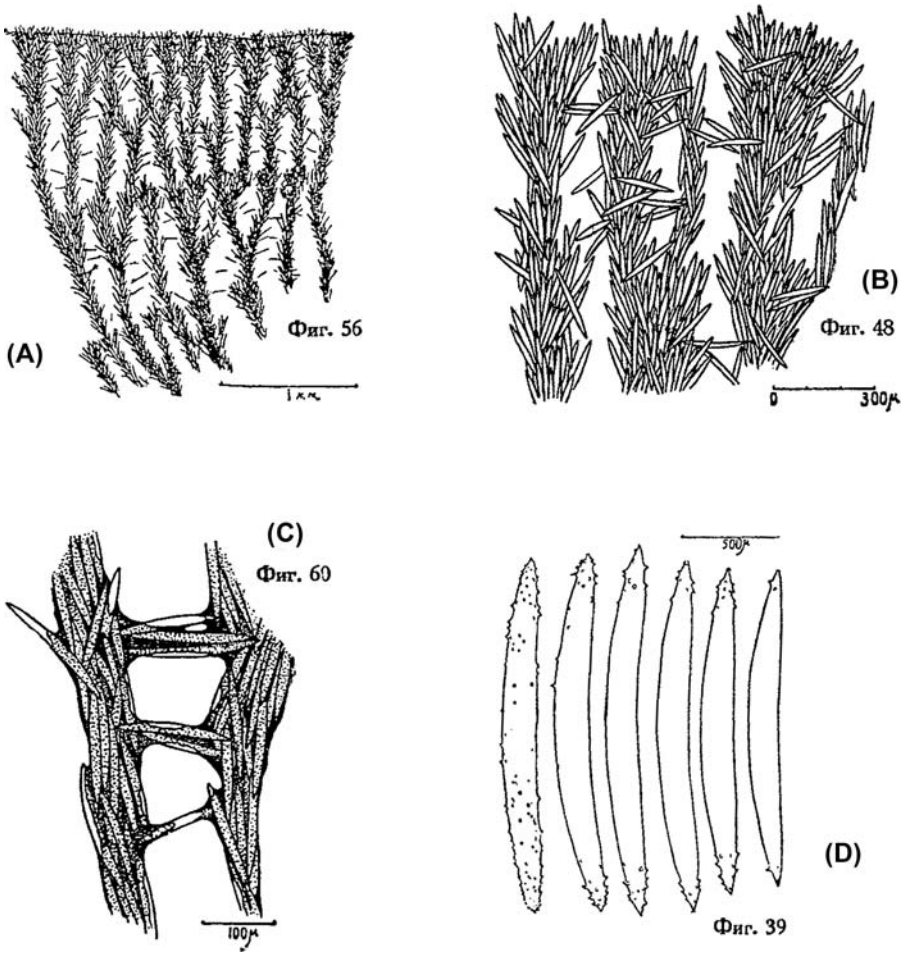


FIGURE 3.53 *Lubomirskia abietina* Swartschewski, 1902. (A) Skeleton architecture; (B) close-up of the ectosomal skeleton; (C) choanosomal skeleton (close-up); (D) spicular complement. *Modified from Rezvoi, 1927.*

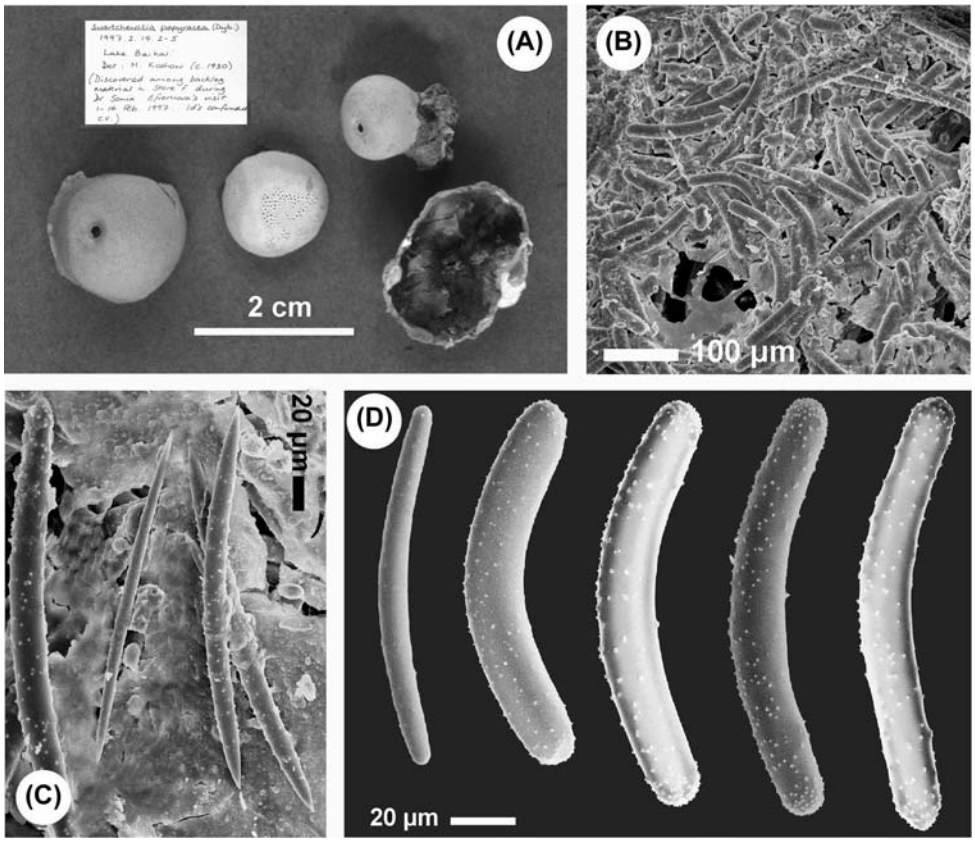


FIGURE 3.54 *Swartschewskia papyracea* Dybowski, 1880. (A) Dry specimens; (B) skeletal architecture; (C) spicules of the inner sponge surface; (D) skeletal spicules. *Modified from Manconi & Pronzato, 2002.*

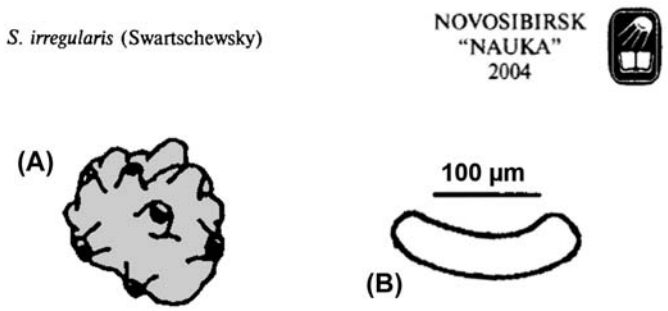


FIGURE 3.55 *Swartschewskia irregularis* (Swartschewski, 1902). (A) Massive growth form; (B) spicular complement. *Modified from Efremova, 2004.*

Spongillida: Lubomirskiidae: *Baikalospongia*: Species

All but one species are endemic to Lake Baikal.

1	Massive to branched	2
1′	Encrusting; smooth surface; spiny strongyles, scattered spines (Fig. 3.56)	*Baikalospongia martinsoni* Efremova, 2004 [Lake Baikal]
2(1)	Branched to massive	3
2′	Pedunculate, to fungiform	4
3(2)	Cushion-like with large lobes; spiny strongyles, large spines only at tips (Fig. 3.57)	*Baikalospongia recta* Efremova, 2004 [Lake Baikal]

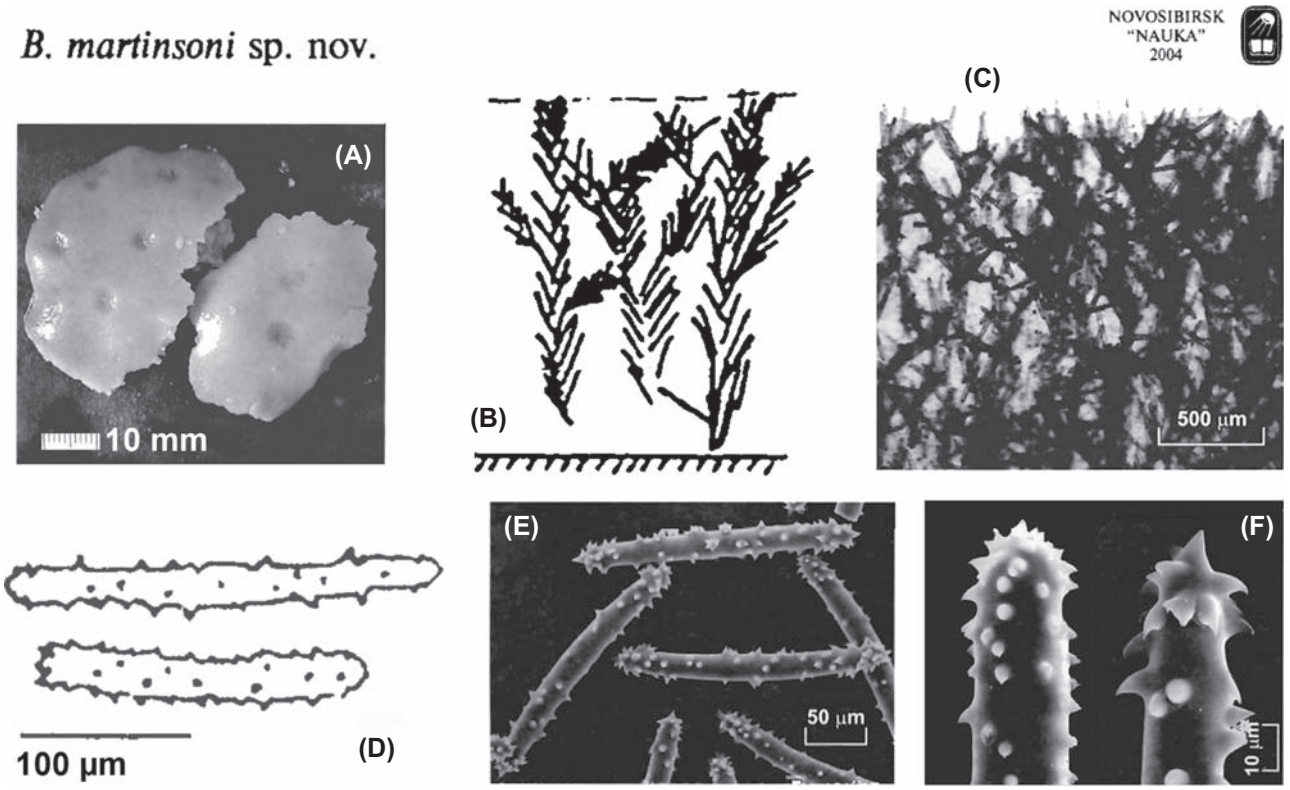


FIGURE 3.56 *Baikalospongia martinsoni* Efremova, 2004. (A) Encrusting growth form (fragments); (B–C) skeletal architecture (cross-section); (D–F) spicular complement. *Modified from Efremova, 2004.*

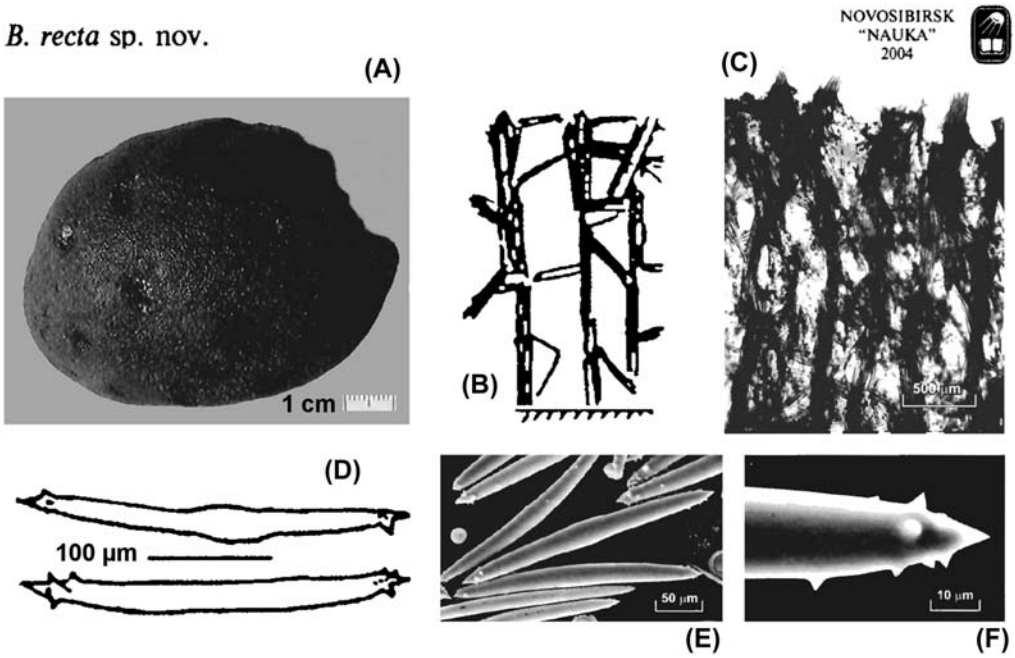


FIGURE 3.57 *Baikalospongia recta* Efremova, 2004. (A) Massive growth form; (B–C) skeletal architecture (cross-section); (D–F) spicular complement. *Modified from Efremova, 2004.*

3′	Massive with cylindrical anastomosing branches; strongyles regularly spiny to smooth (Fig. 3.58) ..... *Baikalospongia dzhegatajensis* Rezvoi, 1927 [Lake Dzhegataj Kul]
4(2)	Rounded with short, large peduncle 5
4′	Fungiform; spiny strongyles, small spines only at tips (Fig. 3.59) ..... *Baikalospongia fungiformis* (Makushok, 1927) [Incompletely described. Lake Baikal]
5(4)	Spiny strongyles with small spines only at tips (Fig. 3.60) ..... *Baikalospongia bacillifera* Dybowski, 1880 [Lake Baikal]
5′	Rounded with short large peduncle; oxeas to strongyles regularly spiny (Fig. 3.61) ..... *Baikalospongia intermedia* Dybowski, 1880 [Lake Baikal]

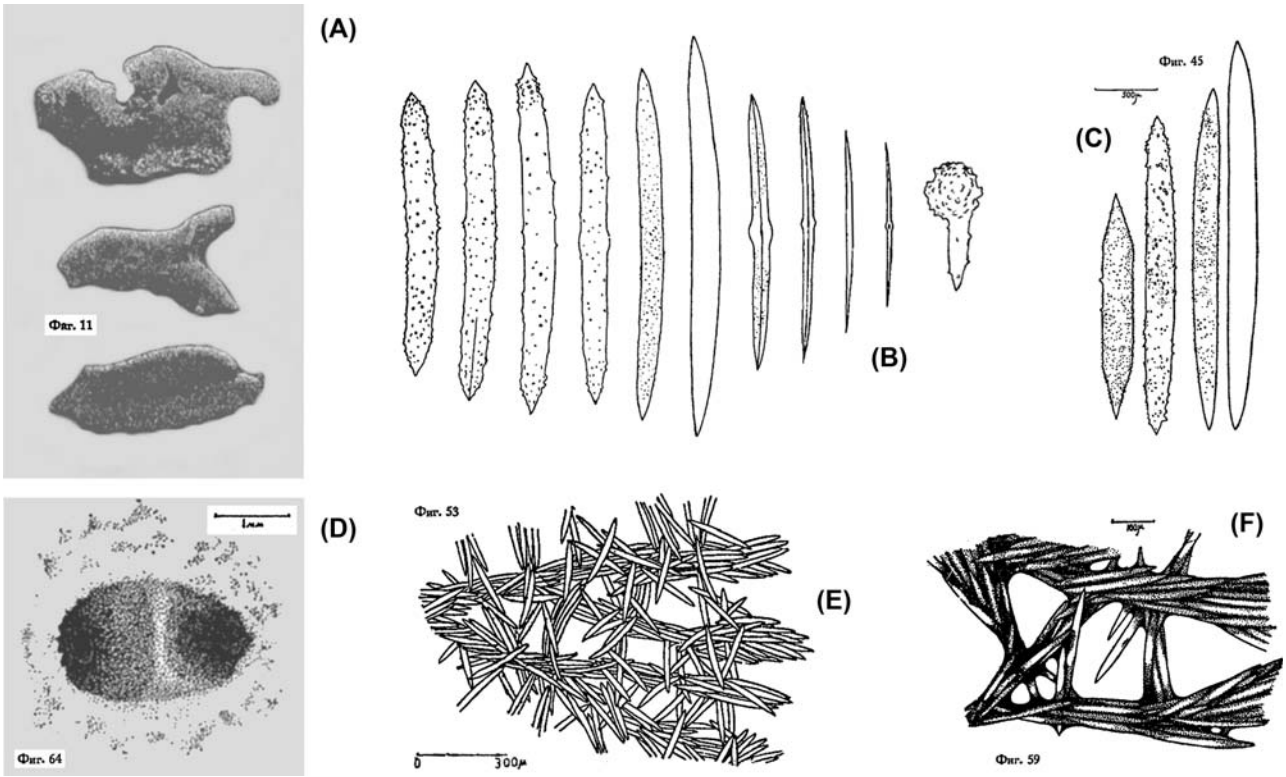


FIGURE 3.58 *Baikalospongia dzhegatajensis* Rezvoi, 1927. (A) Dry specimens; (B–C) spicular complement; (D) sponge osculum; (E) skeleton architecture (sponge surface, right); (F) choanosomal skeleton meshes. *Modified from Rezvoi, 1927, 1936.*

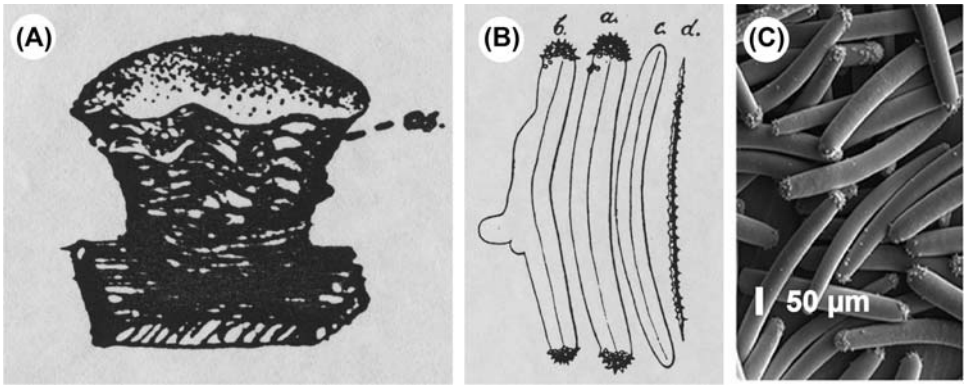


FIGURE 3.59 *Baikalospongia fungiformis* (Makushok, 1927). (A) Schematic drawing of a specimen; (B–C) spicular complement. *Drawings modified from Makuschok, 1927; SEM image modified from Meixner et al., 2007.*

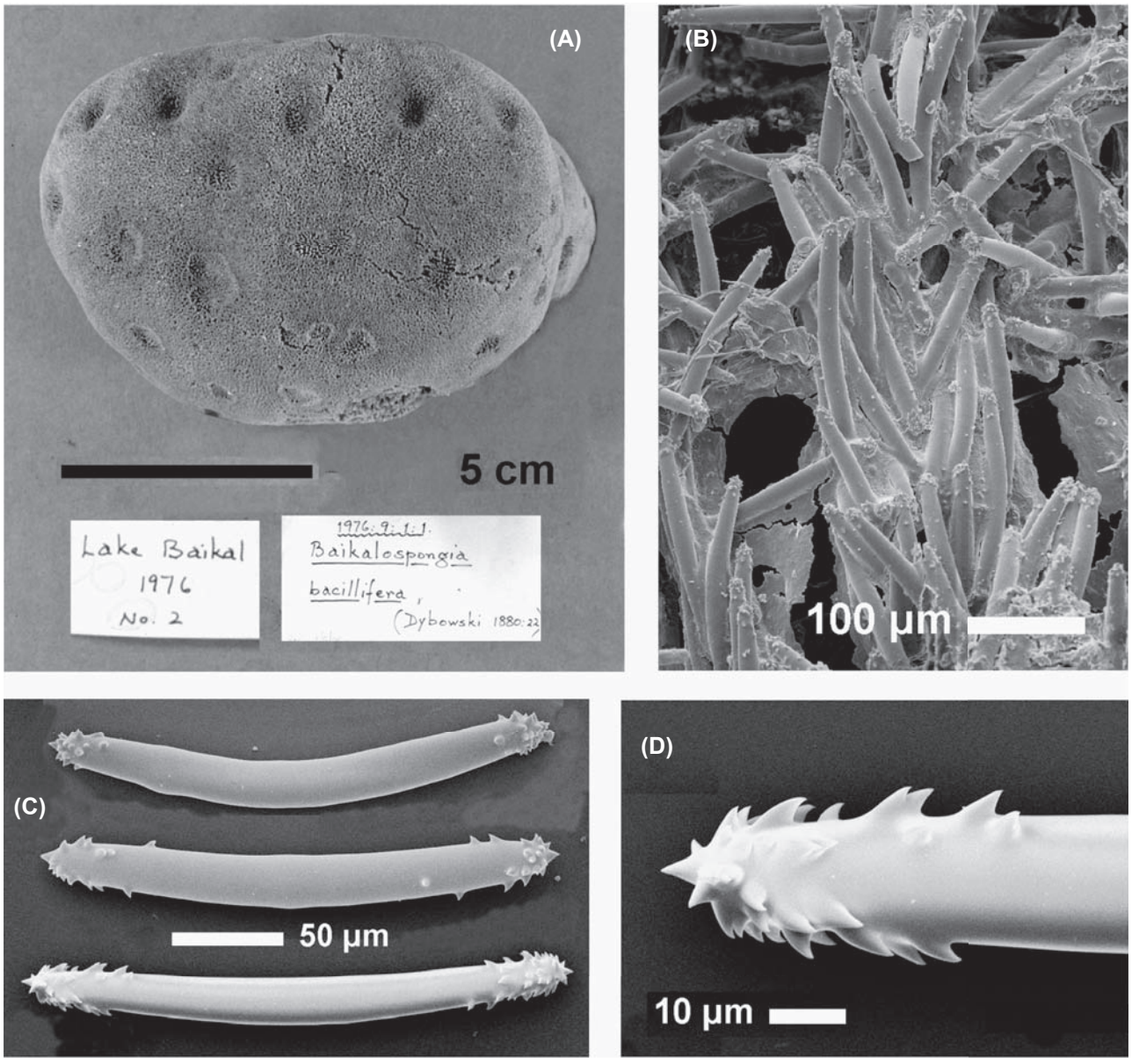


FIGURE 3.60 *Baikalospongia bacillifera* Dybowski, 1880. (A) Massive growth form with typical clusters of oscules; (B) skeleton architecture; (C) spicular complement of strongyles; (D) spiny tip of a spicule. *Modified from Manconi & Pronzato, 2002.*

Spongillida: Malawispongiidae: Genera

1 Megascleres stout, smooth oxeas occasionally with microspines (Fig. 3.62) ..... *Cortispongilla barroisi* (Topsent, 1892)
[Palestinian area: Sea of Galilee and Jordan River]

1′ Megascleres oxeas with very spiny surface ..... ***Ochridaspongia***
[Lake Ohrid]

Spongillida: Malawispongiidae: *Ochridaspongia* Species

Two species endemic to Lake Ohrid.

1 Small mound like sponges settled, in the "interlithon," along the shoreline (Fig. 3.63) ..... *Ochridaspongia interlithonis* Gilbert & Hadzische, 1984
[Incompletely described species]

1′ Large body from globular to massive with outgrowths; abundant in deep water (Fig. 3.64) ..... *Ochridaspongia rotunda* Arndt, 1937

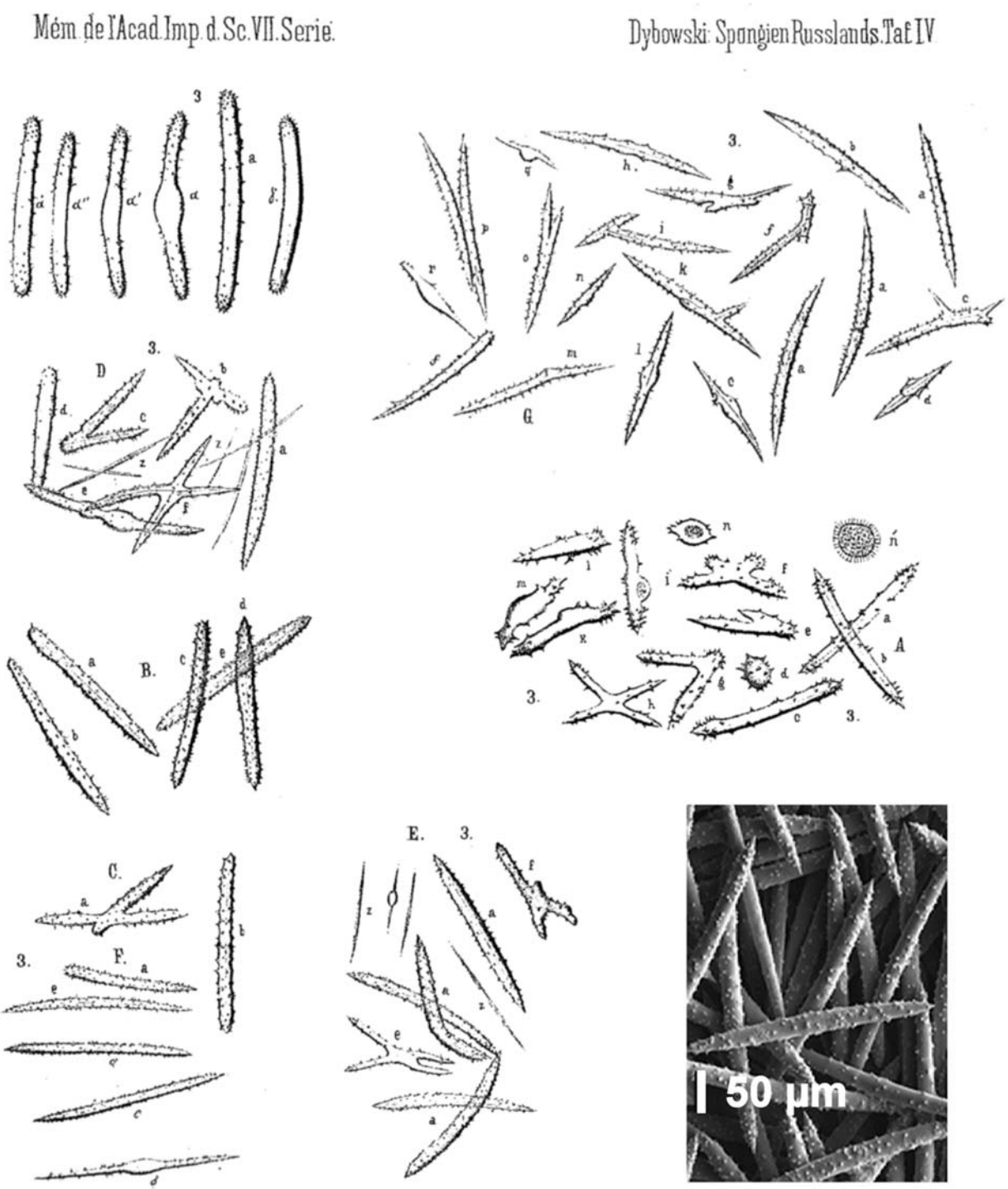


FIGURE 3.61 *Baikalospongia intermedia* Dybowski, 1880. Spicular complement of various specimens. *Drawings modified from Dybowski, 1880; SEM image modified from Meixner et al., 2007.*

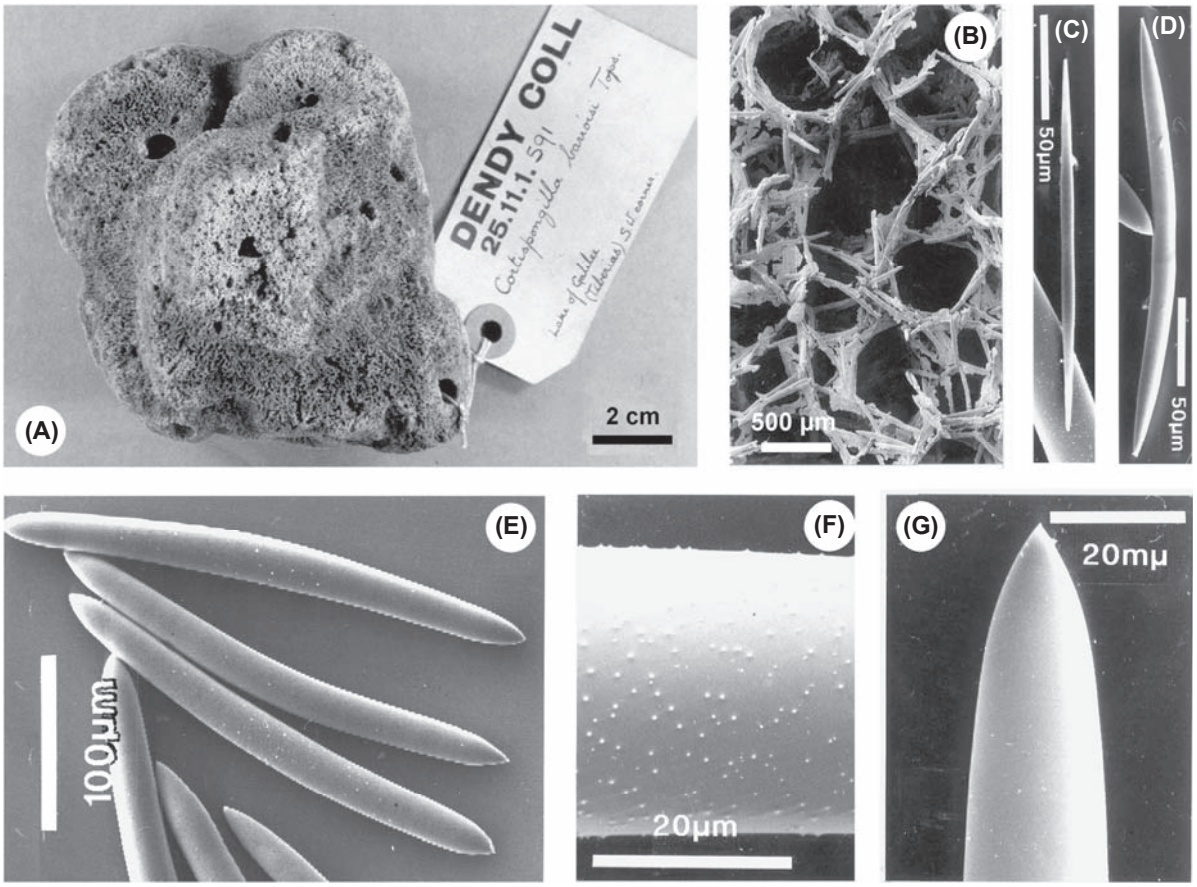


FIGURE 3.62 *Cortispongilla barroisi* (Topsent, 1892). (A) Large dry specimen (Dendy collection, Natural History Museum, London); (B) skeletal network; (C–E) spicules; (F) spicule shaft (close-up); (G) spicule tip (close-up). *Modified from Manconi & Pronzato, 2002.*

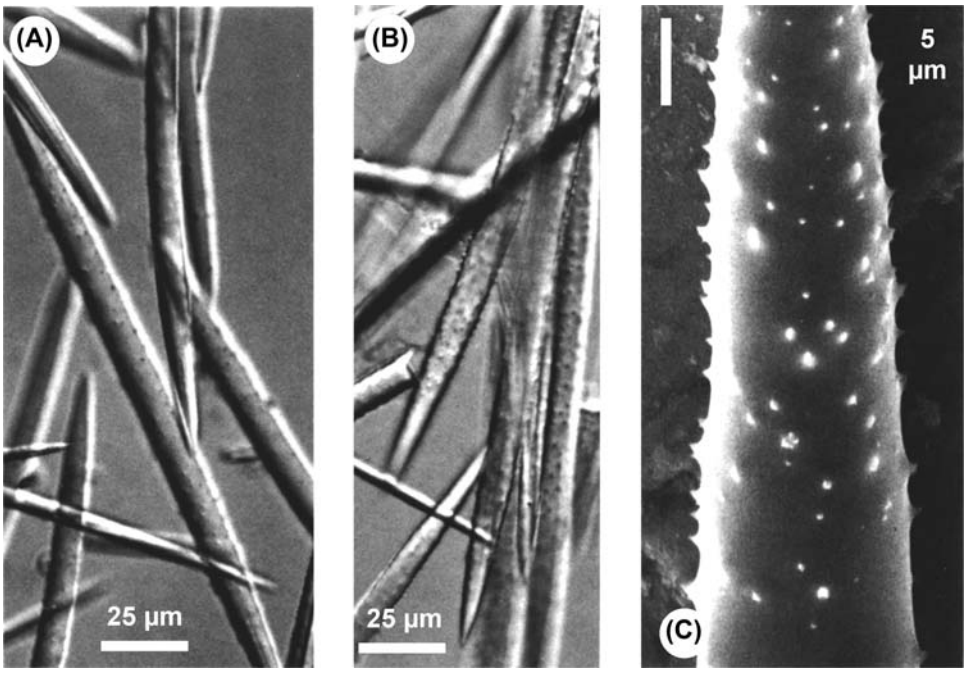


FIGURE 3.63 *Ochridaspongia interlithonis* Gilbert & Hadzische, 1984. (A–B) spicular complement; (C) spicule (close-up). *Modified from Gilbert & Hadzische, 1984.*

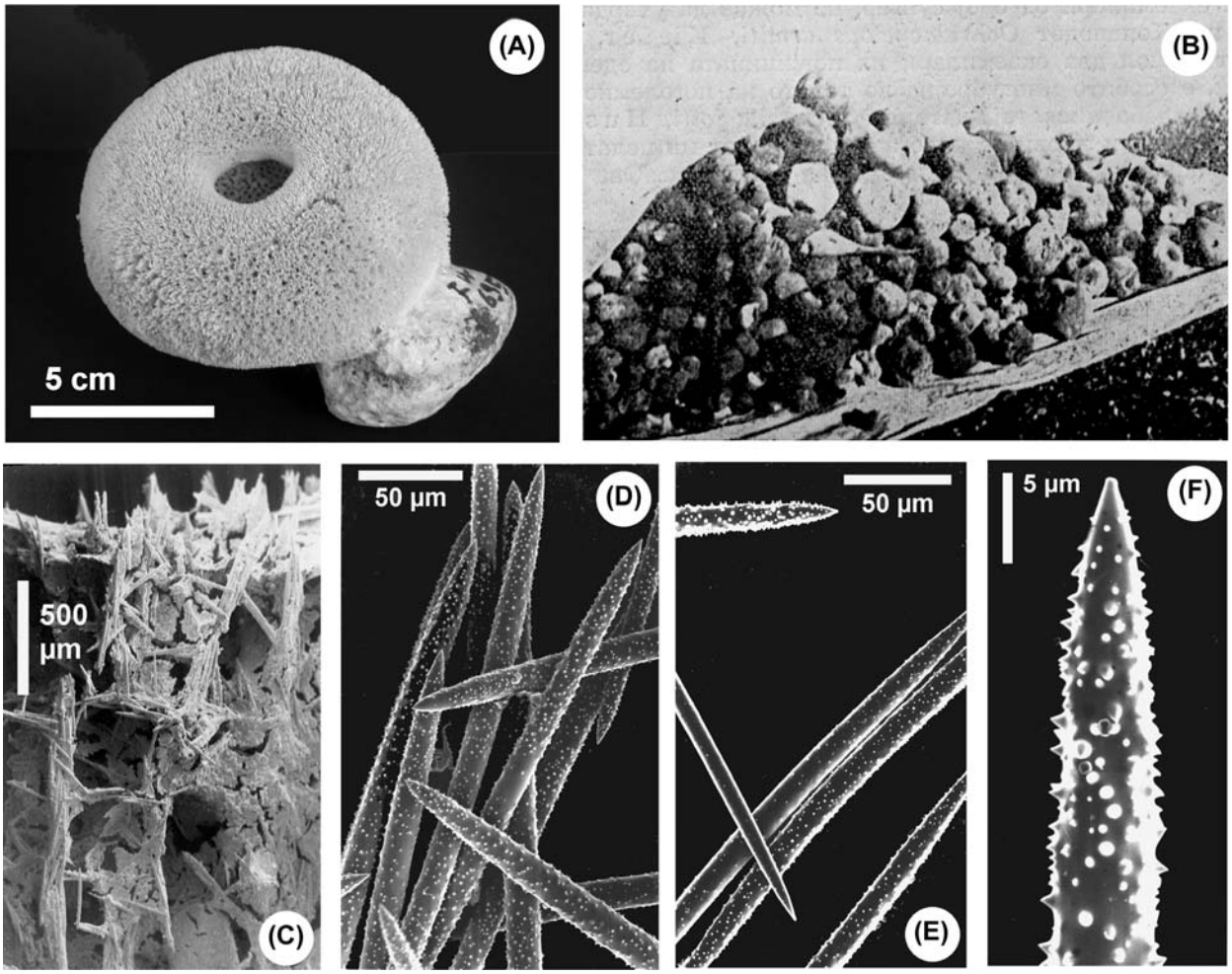


FIGURE 3.64 *Ochridaspongia rotunda* Arndt, 1937. (A) Massive growth form of a dry specimen with large oscular aperture; (B) huge amount of specimens bycatched by nets of professional fishery in the 1950s when this species was very abundant in the Ohrid Lake; (C) choanosomal skeleton architecture (cross-section, lateral view); (D–F) spicular complement. *(B) Modified from Hadzische, 1953; (C–F) modified from Manconi & Pronzato, 2002.*

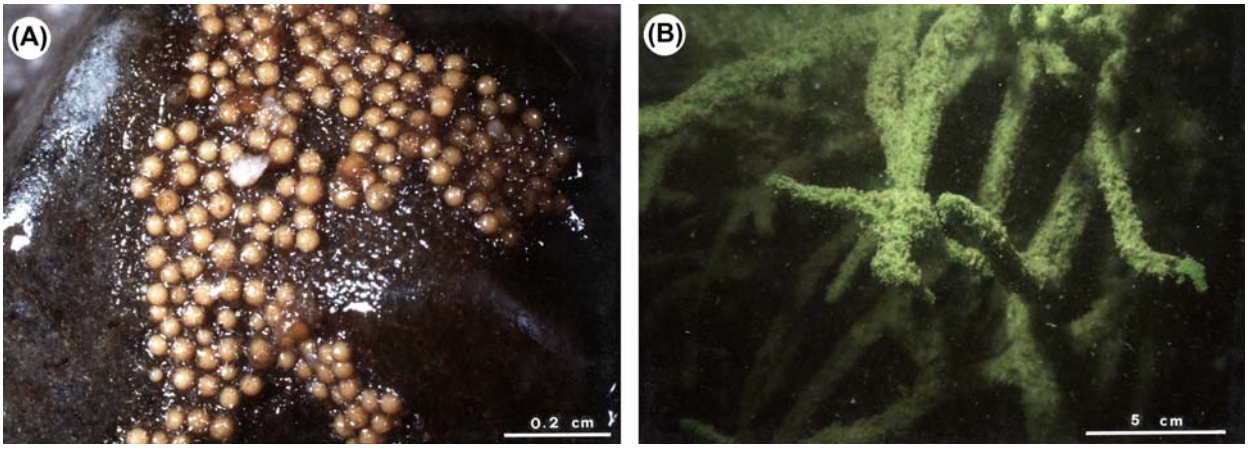


FIGURE 3.65 *Ephydatia fluviatilis* and *Spongilla lacustris* are the only freshwater sponge species described in the Linnaean "Systema Naturae". They are common in the Western Palaearctic inland waters. (A) Carpet of gemmules of *E. fluviatilis*; (B) digitate specimen of *S. lacustris.*

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Chapter 4

Phylum Cnidaria

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INTRODUCTION

Several thousands of cnidarian species are known from all over the world and from all aquatic habitats. Species from fresh water, saline lakes, or fresh estuarine water, however, are very sparse. Disregarding all taxonomic and systematic uncertainty, there are no more than a few dozen species described from inland waters (Jankowski et al., 2008; Dumont, 2009a).

All cnidarians share a simple body plan of a central cavity surrounded by two cellular layers (endoderm, ectoderm). The two layers are separated by a jelly-like mesoglea. Cnidaria utilize nematocysts (stinging cells), which are exclusive to cnidarians, for hunting prey as well as for defense. The life cycle is often complex, including different life cycle stages. Best known are the medusae, often the sexual, motile stage, and the hydranth (hydroid, polyp), often the asexual, sessile stage.

Traditionally, cnidarians are classified into three groups: Anthozoa, Scyphozoa, and Hydrozoa, but recent molecular genetic analysis suggests that there are at least two additional groups, Cubozoa and Staurozoa (Collins et al., 2006). In addition, Polypodiozoa, a parasite of sturgeon fish eggs, are believed to form an additional class. All inland water cnidarians, except *Polypodium*, belong to the class Hydrozoa.

LIMITATIONS

The taxonomy and phylogenetic relationships of hydrozoans in general is unsettled at all levels (Collins et al., 2006). Most hydrozans have a character-poor morphology, coupled with an extraordinary flexibility in shape and strong polymorphism.

The taxonomy of hydras (Hydridae) is controversial and unresolved (Holstein, 1995; Hemmrich at al., 2007; Kawaida et al., 2010). The first classification to include several different genera was developed by P. Schulze (Schulze, 1914, 1917). At present, the most popular is Linné's Linnaeus's one genus taxonomy (Campbell, 1987; Holstein, 1995), which contains all freshwater hydras in the single genus *Hydra*. Campbell (1987) introduced the concept of "groups" within the genus without precisely defining the taxonomic rank of these "groups." Recent molecular data (Hemmrich et al., 2007; Kawaida et al., 2010; Martínez et al., 2010) provide further evidence of a

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high degree of divergence within the Hydridae among the major hydra "groups". Therefore, we suggest using Schulze's classification of hydra species with three genera: *Hydra*, *Chlorohydra*, and *Pelmatohydra*.

The freshwater jellyfish (*Craspedacusta*, *Limnocnida*, and *Astrohydra*) belong to the Olindiidae. Only the polyp stage is known in *Calpasoma*. Because of the similarity of the polyp, *Calpasoma* may be a synonym of *Astrohydra*. There is also some morphological evidence that *Calpasoma* may be a synonym of *Craspedacusta*. Molecular genetic data indicate, however, that *Astrohydra*, *Craspedacusta*, and *Limnocnida* are distinct clades. *Limnocnida* is restricted to Africa, the Himalayan Mountains, as well as southern and southeast Asia. *Astrohydra* is described from Japan, and *Craspedacusta* is reported globally. The medusa stage is clearly morphologically differentiated between the three genera (*Craspedacusta*, *Limnocnida*, and *Astrohydra*), but this is not the case in the hydranth stage. Species status within *Craspedacusta* and *Limnocnida* is somewhat doubtful. Classically, *Craspedacusta* is differentiated into three species: *C. sowerbii* Lankester, 1880, *C. iseanum* Oka & Hara, 1922, and *C. sinensis* Gaw & Kung, 1939 (see Jankowski, 2001). Molecularly, there is strong evidence that *C. sinensis* and *C. ziguiensis* (He & Xu, 1985) differ from other species (Collins et al. 2008). *Craspedacusta sichuanensis* He & Kou, 1984 seems to be a synonym of *C. kiatingi* Gaw & Kung, 1939 (Zang et al., 2009, Fritz et al., 2009) and is supported by the existence of two well-differentiated clades in central Europe, which may correspond to two cryptic species under *C. sowerbii* (Herrera et al., unpublished). *Craspedacusta brevinema* He & Xu, 2002 seems to be a synonym of *C. sinensis*, whereas *C. xinyangensis* He, 1980 seems to be a synonym to *C. sowerbii* (Zang et al., 2009). *Craspedacusta iseanum* is also considered a valid species, but molecular data are lacking. *Craspedacusta chuxiongensis* He et al., 2000 and *C. hangzhouensis* He, 1980 still await verification. It is very likely that *C. kuoi* Shieh & Wang, 1959 represents a variation of *C. sowerbii* (Jankowski, 2001).

Velkovrhia and *Pachycordyle* are in the Bougainvilliidae, but only the hydranth stages are known. *Velkovrhia* is known only from a cave system in Croatia, whereas *Pachycordyle* is only known from Lake Biwa, Japan.

Polypodium is a curious taxon. Some of its life cycle is spent as parasite in sturgeon eggs (Pisces, Acipenseridae, and Polyodontidae). A free living, sexual, and motile stage (medusa) is released during summer months (May−July). *Polypodium* was originally described from Eastern European rivers, but is now known from the Ponto-Caspian basin as well as Northern America (see Bouillion & Boero 2000a,b; Bouillion et al., 2004, Bouillion et al., 2006).

Cordylophora (Clavidae) is an estuarine hydrozoan, which may occasionally occur in relatively fresh water. It was first found in Caspian Sea, but now occurs also in Europe and North America. It grows as a branching colony up to 5 cm high.

Moerisia (Moerisiidae) is generally a marine/estuary genus. *Moerisia lyonsi* was described from Lake Quarun, Egypt. Due to excessive salination, the lake salinity now exceeds that of seawater and *Moerisia* is no longer found there. *Moerisia pallasi* is known from the Caspian Sea.

TERMINOLOGY AND MORPHOLOGY

The terminology follows Slobodkin & Bosser (2001), Buillon et al. (2004), and Dumont (2009a). The basic cnidarian body plan is manifested as either a **polyp** or a **medusa** (Fig. 4.1A(a)B,C). Polyps are typically elongated along the oral/aboral axis. Medusae are campanuliform and usually have their greatest body dimension perpendicular to the oral/aboral axis. The polyp coelenteron (central gastric cavity) is usually deeper than the body is wide, while a medusa is usually wider than the coelenteron is deep. Also, medusae generally have relatively thicker **mesoglea**. In some species, different generations, and, in some cases, the same individual organism at different stages of its development, can adopt either a polyp or a medusa form.

Typically, around the polyp feeding aperture or the medusae bell edge is a ring of tentacles. Exceptions are atentacled hydranths (e.g., *Craspedacusta, Limnocnida*). Tentacles are extensions of the endoderm and ectoderm into more or less elongated projections. The body cavity may or may not extend into the tentacles. Tentacular ectoderm is especially rich in **cnidocyte** cells. Each cnidocyte contains an organelle called a **cnidocyst** or **nematocyst**.

Nematocysts are a specialized cell, responsible for defense and attack (Fig. 4.1A(B)A-M). The cnidocyte apical surface is adorned with a modified cilium, the cnidocil, sensitive to mechanical stimuli. When excited, the **cnidocil** triggers the extremely rapid expulsion of a capsule lodged within the cell, the nematocyst, to the outside. There are at least 15 different types of nematocysts (Fig. 4.1A(B)A-M), all of which bear specific names and are extensively used in the taxonomy of the group. A typical nematocyst is a long, hollow tube (the tubule) that often consists of two sections: a distal thread and often a dilated basal section (butt) with or without barbed hooks. Some types are sticky, and with or without a proteinaceous toxin. Several types may co-occur on a single animal. When everted, nematocysts may penetrate a target organism's integument, and the associated toxin may cause irritation, pain, paralysis, and death.

Medusae and polyps may be solitary or colonial. In fresh water, the hydras are solitary, but all other polyps are at least in part colonial. In colonies, multiple polyps are connected by tubelike hydrocauli. The **hydrocaulus** is the main stem of a hydroid colony. Where the hydrocaulus runs along the substrate, it forms a **stolon** (or **hydrorhiza**) that

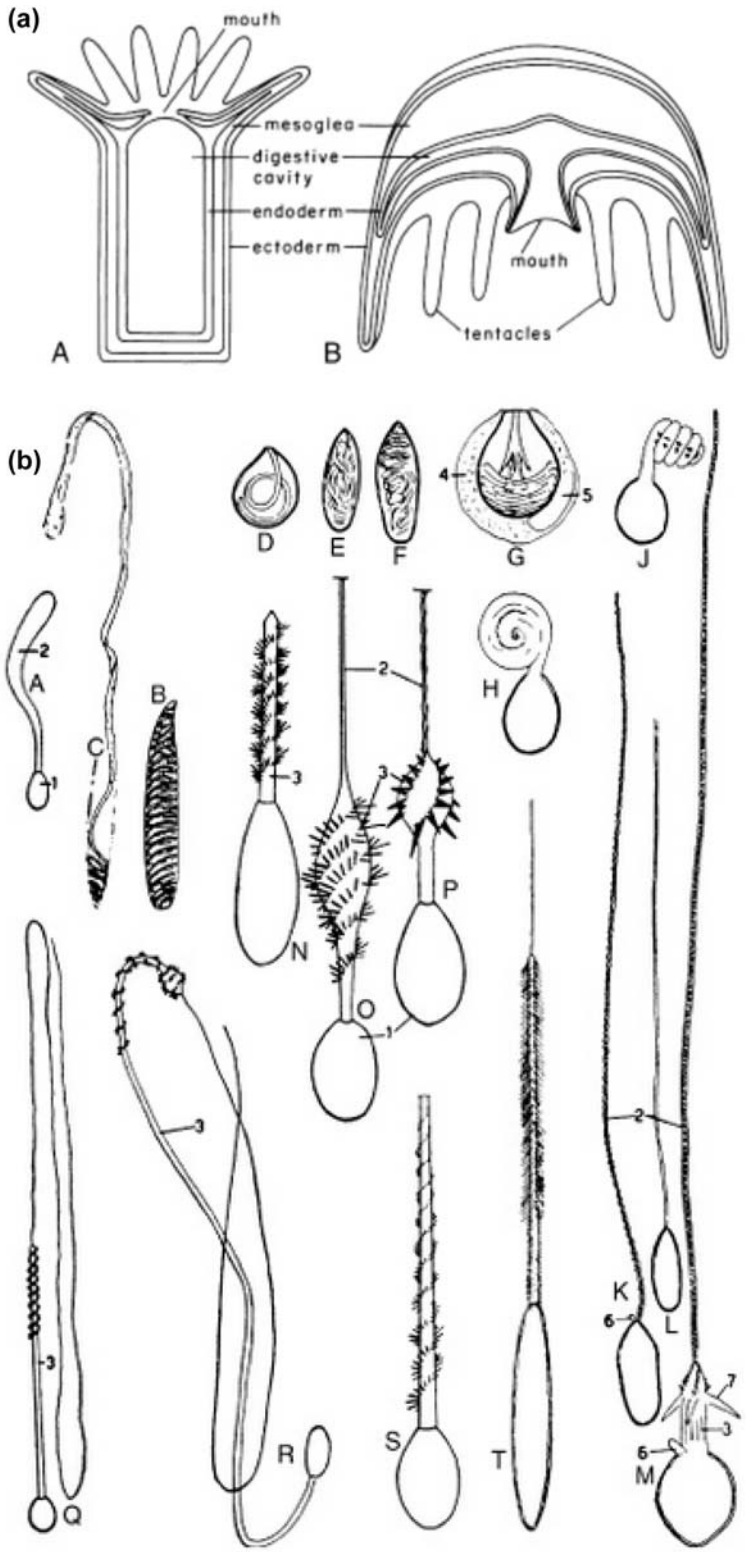


FIGURE 4.1 (a) General body plan of cnidaria ((A) polyp and (B) medusa) and (b) different nematocysts types: (A) rhopalomene (only in Siphonophora), (B) spirocysts, (C) same as (B), (D) desmoneme [(H) and (J) same as (D) but not discharged], (E) atrichous hydrorhiza [(L) same as (E) but not discharged], (F) holotrichous isorhiza [(K) same as (F) but not discharged], (G) stenotele inside its cnidoblast[(M) same as (G) but not discharged], (N) microbasic amastigophore, (O) homotrichous microbasic eurytele, (P) heterotrichous microbasic eurytele, (Q) macrobasic mastigophore, (R) teleotrichous macrobasic eurytele, (S) heterotrichous anisorhiza, (T) microbasic mastigophore; 1 capsule, 2 tube, 3 butt, 4 cnidoblast, 5 its nucleus, 6 lid, 7 stylet. *From Slobodkin & Bossert, 2001.*

anchors the colony. The hydrocaulus is usually surrounded by a sheath of chitin and proteins called the **perisarc**. Perisarcal structures are complex, being mainly composed of chitin and proteins; they are sometimes associated with calcareous elements (coenosteum). The **coenosteum** is a solid, skeletal, spongy material secreted by the coenosarc. The coenosarc is the living tissue overlying the skeletal material.

The perisarcal structure that encloses individual polyps is called the **hydrotheca** (=perisarcal theca). Hydroids in which the hydrotheca surrounds the polyps are called **thecate** (= Leptomedusae); those without hydrotheca are called **athecate** (= Anthomedusae). Such identification, however, is not always easy. Some Anthomedusae polyps are provided with a (gelatinous or membranous) **pseudohydrotheca**, not homologous to perisarcal hydrothecae but similar in function (e.g., some *Bougainvillia* species). Conversely, many Leptomedusae polyps have very reduced thecae or even lack them. In certain colonial forms (*Limnocnida*, *Craspedacusta*), the perisarc is reduced to the basal region and is even lacking in some solitary species such as *Hydra* and *Protohydra*.

A further complication is that many colonies show polymorphism; the members (sometimes called persons) are morphologically specialized for different larvae. At least four different types of **gonophores** are distinguished, according to the degree of development of the medusoid. In the **eumedusoid type** (an almost complete medusa), the development leads to a medusa shape of the gonophore, which will even contain radial canals. A eumedusoid is an almost complete medusa, with **radial canals**, a **subumbrellar space**, sometimes with **manubrium**, but generally without tentacles, sense organs, and velum; some have a free pelagic life. In the eumedusoids, the "gonads" are on the manubrium in anthomedusae and on radial canals in leptomedusae. If accidentally released, these incomplete medusae soon die. The least-advanced type is called a **blastostyle**. In *Pachycordyle kubotai*, gonophores of the eumedusoid type occur, and there have been claims that they are functional. In freshwater species, a dimorphic state is the rule with both feeding and reproductive polyps. The feeding polyps (gastrozoids) look like hydra, whereas the reproductive polyps come in various forms. These reproductive polyps lack tentacles and either bud directly from the hydrocaulus or from another hydranth. In freshwater forms, which are all athecate and where a free medusa stage is often suppressed, such medusoid buds are called gonophores. In some forms the medusae are reduced to sporosacs (fixed gonophores).

In *Limnocnida* and *Craspedacusta*, the polyp (microhydra) is solitary or colonial with an apical field (**hypostome**) of buds instead of tentacles. The hypostome is a mostly domed or conical hydranth apex, always with a terminal mouth. The microhydra produces medusae by a process of lateral budding. Medusae are usually a few millimeters to about 3 cm in diameter. They consist of a bell, the upper side of which is the **exumbrella**, the lower one the **subumbrella**. The bell margin extends inwards to form a circular velum (or **craspedon**). Tentacles, richly endowed with cnidocytes, line the umbrella margin; no cnidocytes occur on the umbrella itself. The mouth opens ventrally at the end of a tube, the manubrium. It leads into a gut or stomach, from which extends four radial canals, joined by a ring canal. The mesoglea forms the bulk of the medusa body; it is elastic, but does not contain cells. Its elasticity, however, allows contractions, commanded by the epitheliomuscular cells, and hence, locomotion by pulsation. Medusae are of separate sexes. The gonads are located in the epidermis of the subumbrella and extend along the radial canals or form a ring around the stomach.

The Hydrozoa have several types of asexual reproductive stages, with asexual reproduction being one of the main characteristics of the group, e.g., budding of planula like bodies, or frustules, of different types (Fig. 4.4 A).

MATERIAL PREPARATION AND PRESERVATION

Hydroids

Fresh and brackish water hydroids can be collected by hand from a boat and from shore from different hard substrates (aquatic plants, snags, stones). Animals can be collected also by scuba or free diving.

Polyps are fixed in 4%–5% formaldehyde or 70% ethanol (for morphological study) or in 99% ethanol (for DNA extraction and molecular investigations). Many hydroids are not identifiable if not fertile. Therefore, live specimens can be cultured in small aquaria and Petri dishes containing water from the sampling site with daily examination for reproductive activity. The animals can survive like this for 3–4 days or more.

Nematocyst studies are best conducted on fresh animals using light microscopy with 40x and oil immersion 100x objectives. To observe nematocyst morphology, transfer a piece of polyp with tentacles to a microscope slide in a drop of water and squash preparation using a cover slip. If possible, about 5–10 undischarged capsules of each nematocyst type should be measured (maximum length and maximum width). For details, see Campbell (1983).

Medusae

As described in Bouillion et al. (2006), gelatinous plankton are very fragile and easily damaged. Hydromedusae can be caught by plankton nets that are very slowly towed for about 10–20 min. Net mesh sizes should be about 200–250 µm; larger meshes may allow small

specimens to escape, while nets with smaller meshes may become clogged and the specimens damaged. The net aperture should be from 30 cm to 1 m, depending on the power of the vessel; much wider openings are used in open and deep water, where the fauna is sparse. In areas very rich in plankton, a hand net or even a bucket may be used.

It is better to fix the medusae immediately in 4%–5% formaldehyde or in 99% ethanol (for DNA extraction and molecular investigations). The material should be brought rapidly to the laboratory, shielded from direct sunlight, and kept as cool as possible. Specimens should be examined under a stereomicroscope and medusae individually removed with wide-mouthed pipettes and placed in finger bowls of clear water. This method is the most rewarding, allowing both the observation of the characters of the living animals and a perfect fixation.

Medusae nematocyst examination is conducted as was described above for hydroids.

KEYS TO CNIDARIA

Cnidaria: Classes

1 Endocellular parasitic stages producing free living tentacled medusa stages with atrichous isorhiza nematocysts (Figs. 4.2 B) ..... Polypodiozoa: Polypodiidae: one species: *Polypodium hydriforme* Ussov, 1885 [Iran, Ponto Caspian. Introduced to Nearctic]

1′ Free living hydroid or medusae lacking atrichous isorhiza nematocysts ..... **Hydrozoa [p. 97]**

Hydrozoa: Families

Modified after Bouillion et al., (2004, 2006).

1 Hydroids 2

1′ Medusae 6

2(1) Hydranth solitary or colonial, usually rather conspicuous; sometimes with a coenosteum; mostly with desmonemes nematocysts (Fig. 4.1 B); typically athecate, without a rigid perisarcal hydrotheca covering the hydranth body, a gelatinous or membranous pseudohydrotheca may sometimes cover the base of the hydranth, adhering closely to the ectoderm (Anthomedusa) (Fig. 4.3) 3

2′ Hydranth small, sessile; generally solitary or forming small reptant or bipolar colonies; never with desmoneme nematocysts (Fig. 4.1 B); very simple; with or without tentacles; often close to planula structure and budding planula-like structures or frustules (Fig. 4.4 A); body plans range from: forms without mouth and permanent gastric cavity (=feeding planula) to forms with mouth and hypostome, but without tentacles, forming transitory colonies or definitive colonies with a limited number of individuals to forms with hypostome and tentacles; no perisarcal thecae, but cysts and stolons covered by chitin (Fig. 4.4) ..... **Olindiidae [p. 99]**

3(2) Hydranth with filiform tentacles; hydranth with conical or rounded hypostome; colonies without massive calcareous coenosteum; dactylozooid nematocysts (Fig. 4.1 B) absent (Filifera) 4

3′ Hydranths usually with capitate tentacles either in the adult polyps or during their larval life; gonophores generally borne on hydranth body (Capitata) 5

4(3) Hydranth with tentacles in distal (oral) whorls only ..... **Bougainvilliidae [p. 102]**

4′ Hydranth with tentacles scattered all over the body; colonies erect or stolonal (Figs. 4.3 A–C) ..... Clavidae, one species: *Cordylophora caspia* Pallas, 1771 [Palaearctic. Introduced to Nearctic]

5(4) Hydranth with filiform or modified moniliform tentacles, in one whorl under hypostome; living in fresh water (Fig. 4.5) ..... **Hydridae [p. 102]**

5′ Hydranth with moniliform or modified moniliform tentacles scattered or in one whorl around middle part of body; living in brackish or salt water (Fig. 4.3 G) ..... Moerisiidae, one genus; ***Moerisia*** **[p. 105]**

6(1) Medusa without statocysts; gonads on manubrium, occasionally extending for a short distance along basal region of radial canals; marginal tentacles solid or hollow; usually with tentacular bulbs; umbrella generally entire; with radial and circular canals; sense organs, when present, ocelli; umbrella typically campanuliform; with desmonemes; with hydroid stage (Figs. 4.3 F, H, Anthomedusae) ..... Moerisiidae, one genus; ***Moerisia*** **[p. 105]**

6′ Medusa with ectoendodermal statocysts; gonads on radial canals, exceptionally on manubrium; marginal tentacles hollow; without tentacular bulbs; umbrella entire; with radial and circular canals; with statocysts enclosed into the mesoglea near ring canal or in the velum; without desmonemes; with hydroid stage (Limnomedusae) ..... **Olindiidae [p. 99]**

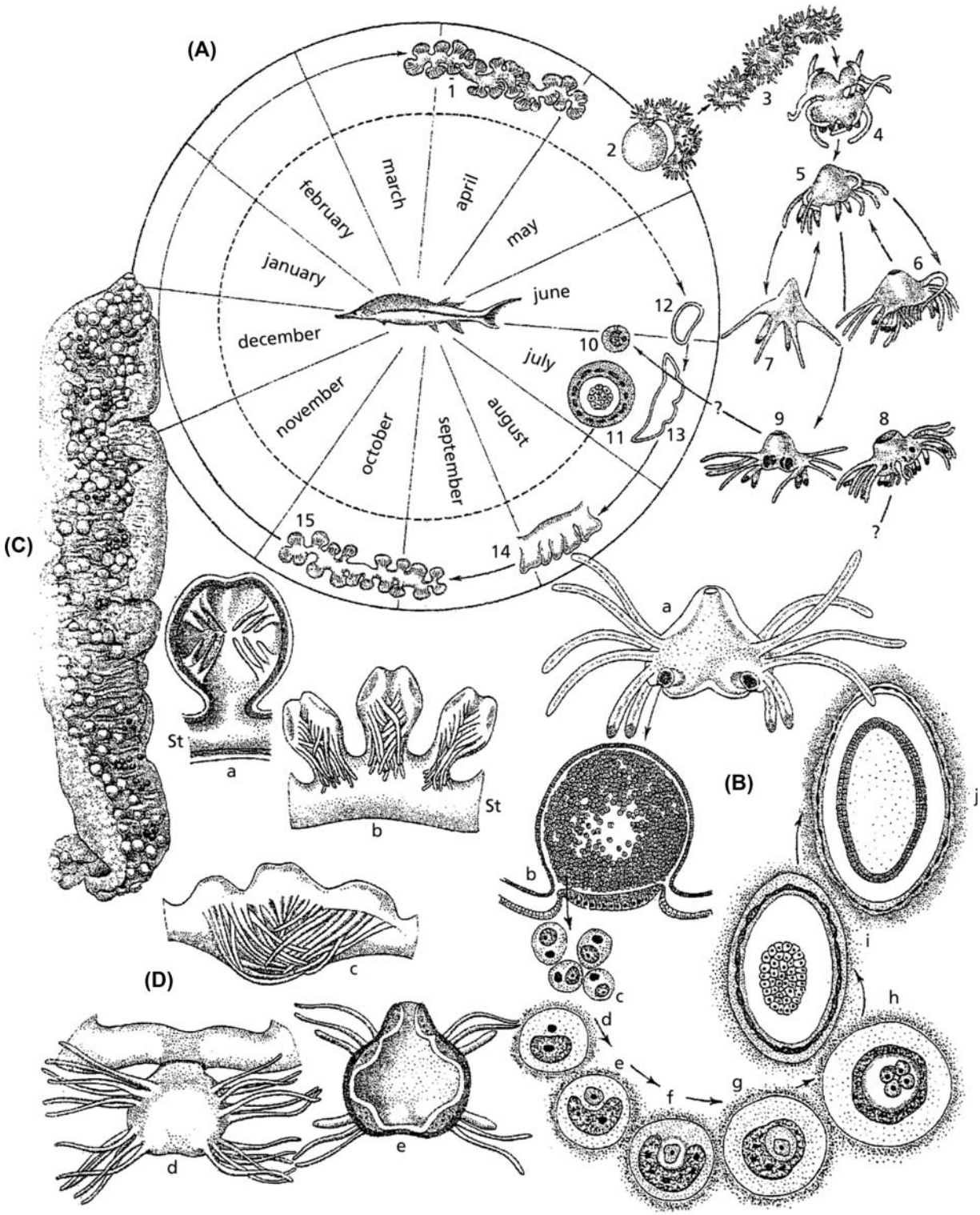


FIGURE 4.2 Life cycle of *Polypodium hydriforme* (Ussov, 1887).

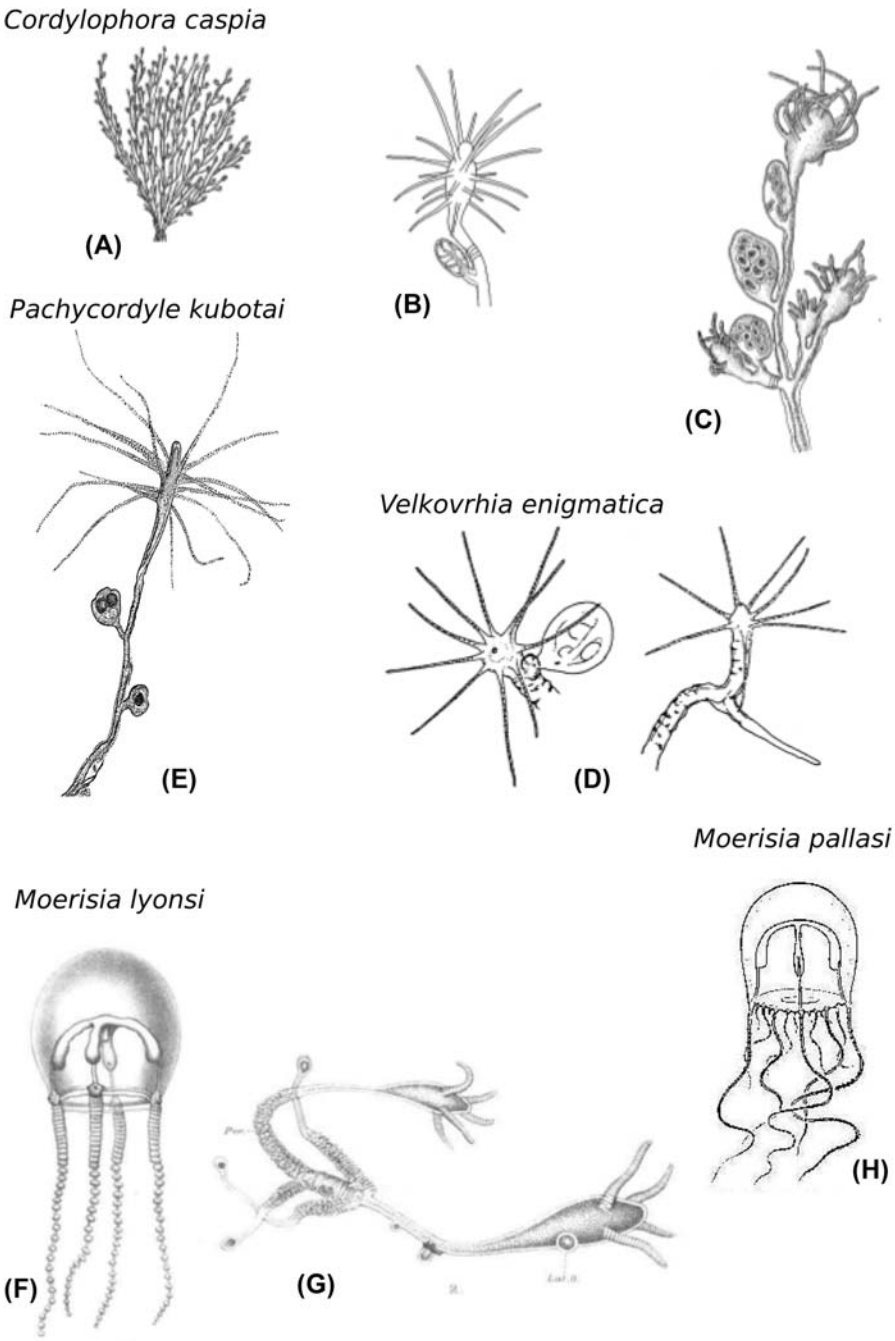


FIGURE 4.3 Life-stages of different inland water anthomedusan ((A–D) Bouillion et al., 2006; (E) B. Anokhin; (F–H) Boulenger, 1908).

Hydrozoa: Olindiidae: Genera

The hydroid stage is known for a few genera only. Bouillion et al. (2006) state that differentiation between *Craspedacusta* and *Limnocnida* hydroids is not possible. A handful of medusa genera from inland waters have been described (Jankowski, 2001), many insufficiently, and hence their status is doubtful. However, molecular analysis strongly indicates that *Astrohydra, Craspedacusta*, and *Limnocnida* are valid (Collins et al. 2006). This key is modified from Hashimoto (1981) and Bouillion et al. (2006).

1	Hydroids	2
1′	Medusae	4
2(1)	Hydroid as a rule colonial; without tentacles	3

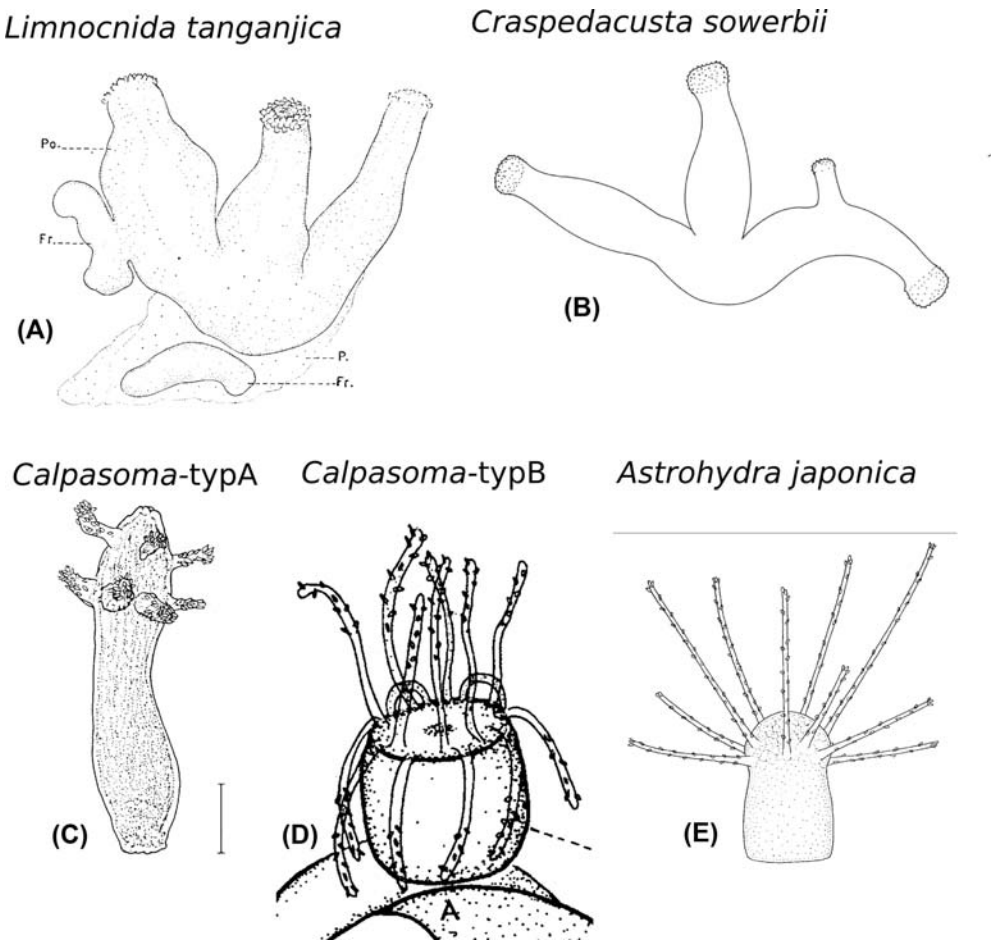


FIGURE 4.4 Hydranths of (A) *Limnocnida* (Bouillion, 1957), (B) *Craspedacusta* (Pennak, 1953), (C) *Calpasoma*-TypA (Holstein, 1995, according to Fuhrmann 1939), (D) *Calpasoma*-TypB (Matthews, 1966, according to Buchert, 1960) and (E) *Astrohydra* (Hashimoto, 1981). *(A, C—E) From Jankowski 2001*.

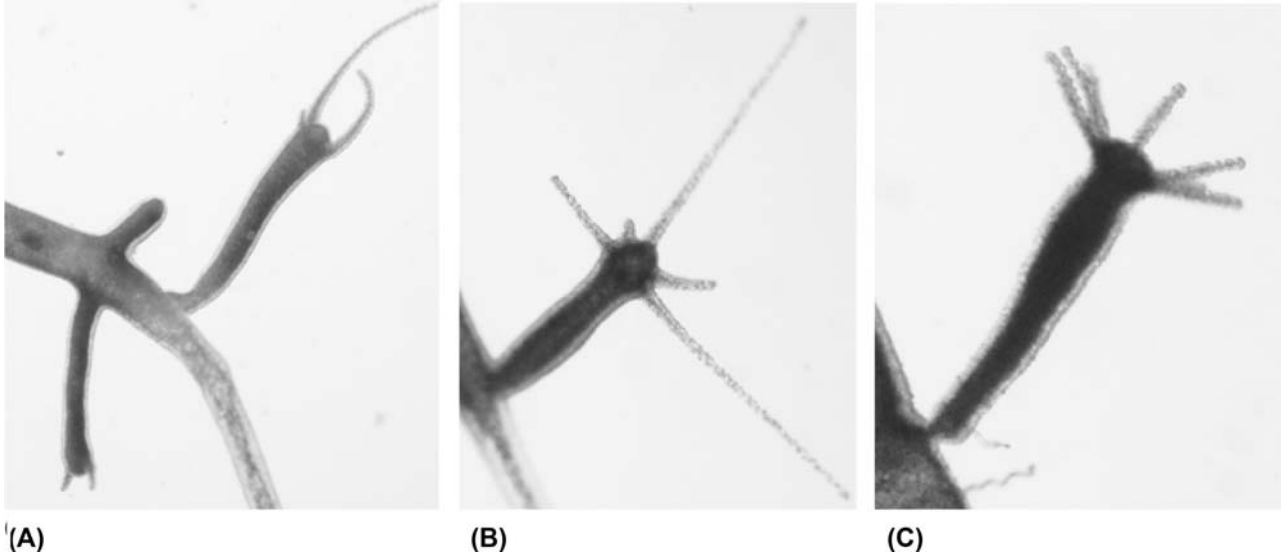


FIGURE 4.5 Comparison of tentacle origin on buds. (A and B) Lateral tentacles arising conspicuously early (e.g., *Pelmatohydra oligactis*); (C) Tentacles arising simultaneously (e.g. *Hydra circumcincta*).

2′	Hydroid as a rule solitary; with fine tentacles (Figs. 4.4 C–E)	*Astrohydra/Calpasoma*
3(2)	Hydroid hypostome with 2–3 encircling papillae rows (Fig. 4.4 A)	***Limnocnida*** **[p. 101]**
3′	Hydroid hypostome without papillae but armored with uniform nematocysts (Fig. 4.4 B)	***Craspedacusta*** **[p. 101]**
4(1)	Tentacles without unicellular long and straight bristle-like expansions	5
4′	Up to 29 hollow marginal tentacles without marginal bulbs, each bearing many unicellular long and straight bristle-like expansions with 1–3 cnidocysts apically; manubrium quadrangular; mouth with four small lips; radial canals usually four; up to 15 spherical statocysts; only juvenile known (Fig. 4.10)	***Astrohydra*** **[p. 106]**
5(4)	Gonads on manubrium, circular; statocysts spherical, enclosed in umbrellar margin mesoglea (Fig. 4.11)	***Limnocnida*** **[p. 101]**
5′	Gonads on radial canals (Fig. 4.12); statocysts in elongated vesicles enclosed in velum (Fig. 4.13)	***Craspedacusta*** **[p. 101]**

Hydrozoa: Olindiidae: *Limnocnida*: Species

The hydroid stages of *Limnocnida* species are not separable. Six species have been described (Jankowski, 2001), however, only one, *L. tanganjica* Günther, 1893, occurs in the Palearctic. A second species, *L. nepalensis* Dumont, 1976, has been described from the Himalayan Mountains and, hence, is also considered.

1	Statocyst/tentacle index ~0.2 (Figs. 4.11 C, D, F) [Himalayas]	*Limnocnida nepalensis* Dumont, 1976
1′	Statocyst/tentacle index ~0.8 (Figs. 4.11 A, B, E) [Africa]	*Limnocnida tanganjica* Günther, 1893

Hydrozoa: Olindiidae: *Craspedacusta*: Species

The hydroid stages of *Craspedacusta* species are not separable. A number of species were described during the last 100 years. Classically, *Craspedacusta* is differentiated into three species: *C. sowerbii*, *C. iseanum*, and *C. sinensis*. However, modern molecular genetic studies indicate more differentiation, which corresponds, at least in parts, with morphological types (Jankowski, 2001, Collins et al. 2008, Zang et al., 2009, Fritz et al., 2009, Herrera et al., unpublished). Revision is needed.

1	Statocyst tubular (Figs. 4.13 A–E)	2
1′	Statocyst spherical; nematocysts on tentacles are scattered; low number of tentacles (Figs. 4.13 F, G) [Asia: Japan: Province Ide; unrecognizable]	*Craspedacusta iseanum* Oka & Hara, 1922
2(1)	Nematocyst warts arranged regularly (Figs. 4.14 A–D, F, K)	3
2	Nematocyst warts arranged irregularly (Figs. 4.14 I, L, M)	5
3(2)	Nematocyst warts in a ring	4
3′	Nematocyst warts horseshoe-like (Figs. 4.12 G and 4.14 K) [Asia: China: Province Hubei]	*Craspedacusta ziguiensis* He & Xu, 1985
4(3)	Gonads brownish yellow (Figs. 4.12 A, B) [Worldwide]	*Craspedacusta sowerbii* Lankester, 1880
4′	Gonads green (Fig. 4.12 D) [Asia: China: Province Henan]	? *Craspedacusta kiatingi* Gaw & Kung, 1939
5(2)	Perradial tentacles longer than other tentacles	6
5′	Perradial tentacles not longer than other tentacles (Fig. 4.12 E) [Asia: China: Provinces Hubei and Sichuan]	*Craspedacusta sinensis* Gaw & Kung, 1939
6(5)	Gonads flattened, pocket-like, twisted, with a digitate projection (Fig. 4.12 H) [Asia: China: Provinces Henan]	? *Craspedacusta chuxiongensis* He et al., 2000
6′	Gonads band-shaped or foliform without digitate projection (Fig. 4.12J) [Asia: China: Province Zhejiang]	? *Craspedacusta hangzhouensis* He, 1980

Hydrozoa: Bougainvilliidae: Species

Medusa stages, if present, are unknown.

1 Two to four alternating close whorls of tentacles beneath hypostome; sporosacs or eumedusoids on stem; colonies well developed, creeping, with branched or unbranched hydrocauli; perisarc terminating at base of hydranth; hydranths clavate to fusiform, with 2–4 alternating close whorls of filiform tentacles beneath hypostome, hypostome convex; gonophores borne on stem, as fixed sporosacs or free eumedusoids without marginal tentacles, mouth or oral tentacles, radial canals or ring canal, seldom with velum, manubrium simple surrounded by gonads, no sense organs; they correspond to highly reduced medusae, resembling medusoid forms of siphonophores (Fig. 4.3 E) ..... *Pachycordyle kubotai* Stepanjants et al., 2000 [Japan; endemic to Lake Biwa]

1′ Hydranths erect, covered by perisarc; hydranths with two whorls of filiform tentacles, no pseudohydrothecae; gonophores on hydrocauli, as styloid fixed sporosacs; endemic to cave lakes (Fig. 4.3 D) ..... *Velkovrhia enigmatica* Matjasic & Sket, 1971 [Slovenia]

Hydrozoa: Hydridae: Genera

1 Live animal not green, apical part of holotrichous isorhiza nematocysts (Fig. 4.1 B) not narrower than basal part or only slightly more narrower 2

1′ Live hydra green due to intracellular algae symbionts; apical part of holotrichous isorhiza nematocysts distinctly more narrow than basal part ..... ***Chlorohydra*** **[p. 102]**

2(1) Hydra with distinct stalk, normally more transparent than the body; buds acquire two lateral tentacles before other tentacles appear (Figs. 4.5 A, B); holotrichous isorhizas without transverse coils ..... ***Pelmatohydra*** **[p. 103]**

2′ Hydra without distinct stalk; buds acquire tentacles in some other order (Fig. 4.5 C); holotrichous isorhizas with transverse coils ..... ***Hydra*** **[p. 103]**

Hydrozoa: Hydridae: *Chlorohydra*: Species

1 Holotrichous isorhizas tubule with proximal part coiled in 3 or 4 transverse loops (Figs. 4.6 and 4.9 A) ..... *Chlorohydra viridissima* Pallas, 1766

1′ Holotrichous isorhizas tubule with proximal part coiled in 2 or (rarely) 3 transverse loops (Figs. 4.6 and 4.9 B) ..... *Chlorohydra sinensis* Wang et al., 2009

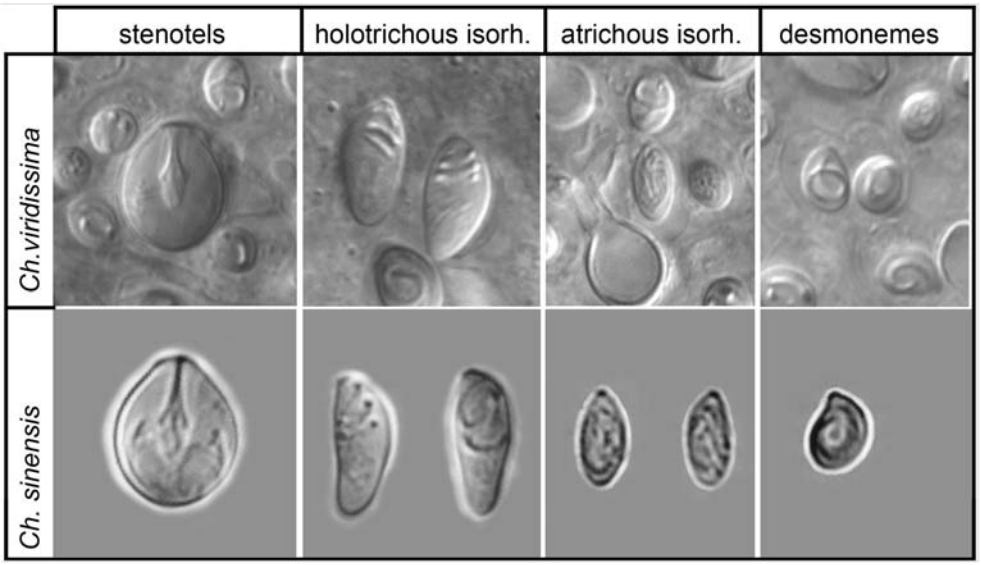


FIGURE 4.6 Nematocysts of *Chlorohydra* species. For *Ch. sinensis* after Wang et al. (2009).

Hydrozoa: Hydridae: *Pelmatohydra*: Species

1 Hydra from continental Eurasia 2

1′ Hydra from Japan (Figs. 4.7 and 4.9 C) ..... *Pelmatohydra robusta* Itô, 1947

2(1) Holotrichous isorhizas 2.3−2.8 times as long as broad (Figs 4.7 and 4.9 D) ..... *Pelmatohydra oligactis* (Pallas, 1766) [Palaearctic. Nearctic]

2′ Holotrichous isorhizas less than 2.3 times as long as broad (Figs. 4.7 and 4.9 E) ..... *Pelmatohydra baikalensis* (Swarczewsky, 1923) [Russia: Lake Baikal]

Hydrozoa: Hydridae: *Hydra*: Species

Some species cannot be distinctly recognized by morphology alone. In these cases only regional identification is possible. The taxon *Hydra magnipapillata* Itô, 1947 is widely used in laboratories for various analytical purposes. Martinez et al. (2010) have shown that *H. magnipapillata* is conspecific with *H. vulgaris*.

1 Stenotele nematocysts (Fig. 4.1 B) plump, less than 1.5 times as long as broad 2

1′ Stenotele nematocytes at least 1.5 times as long as broad (Figs. 4.8 and 4.9 F) ..... *Hydra oxycnida* Schulze, 1914

2(1) Holotrichous isorhiza nematocytes plump, less than 1.6 times as long as broad (Fig. 4.8); embryonic thecae attaches to a substratum 3

2′ Holotrichous isorhiza nematocytes slender, more than 1.6 times as long as broad (Fig. 4.8); embryonic thecae not attached to a substratum 4

3(2) Hydras not from China (Fig. 4.9 G) ..... *Hydra circumcincta* Schulze, 1914.

3′ Hydras from China ..... *Hydra harbinensis* Fan & Shi, 2003

4(2) Hydras from China 5

4′ Hydras not from China (Fig. 4.9 G) ..... *Hydra vulgaris* Pallas, 1766

5(4) One type of holotrichous isorhiza: holotrichous isorhizas tubule proximal part coiled transversely (Fig. 4.8) *Hydra daqingensis* Fan, 2000

5′ Two types of holotrichous isorhiza: holotrichous isorhizas tubule proximal part coiled transversely (type A) or coiled irregularly and longitudinally (type B) (Fig. 4.8) ..... *Hydra beijingensis* Fan, 2002

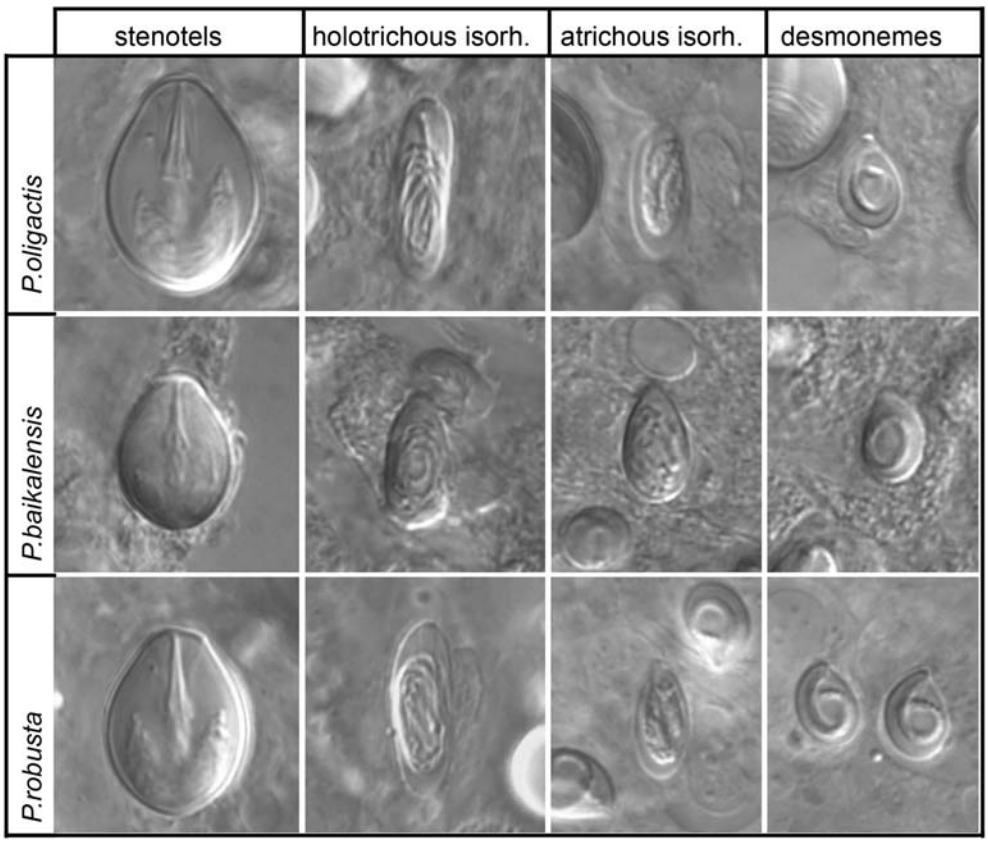


FIGURE 4.7 Nematocysts of *Pelmatohydra* species.

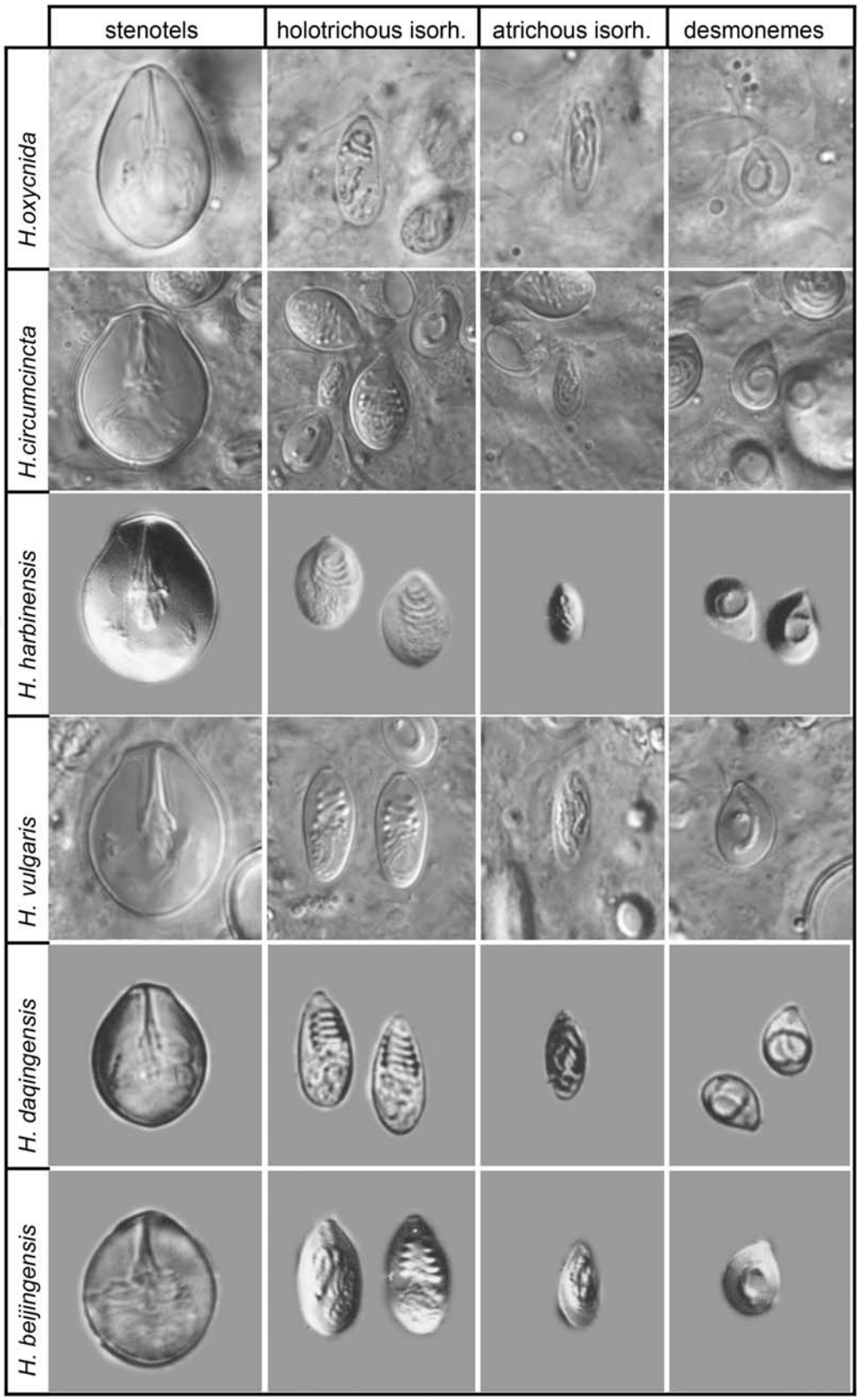


FIGURE 4.8 Nematocysts of Hydra species. *H. harbinensis* after Fan & Shi (2003), *H. daqingensis* after Fan (2000), *H. beijingensis* after Fan (2003).

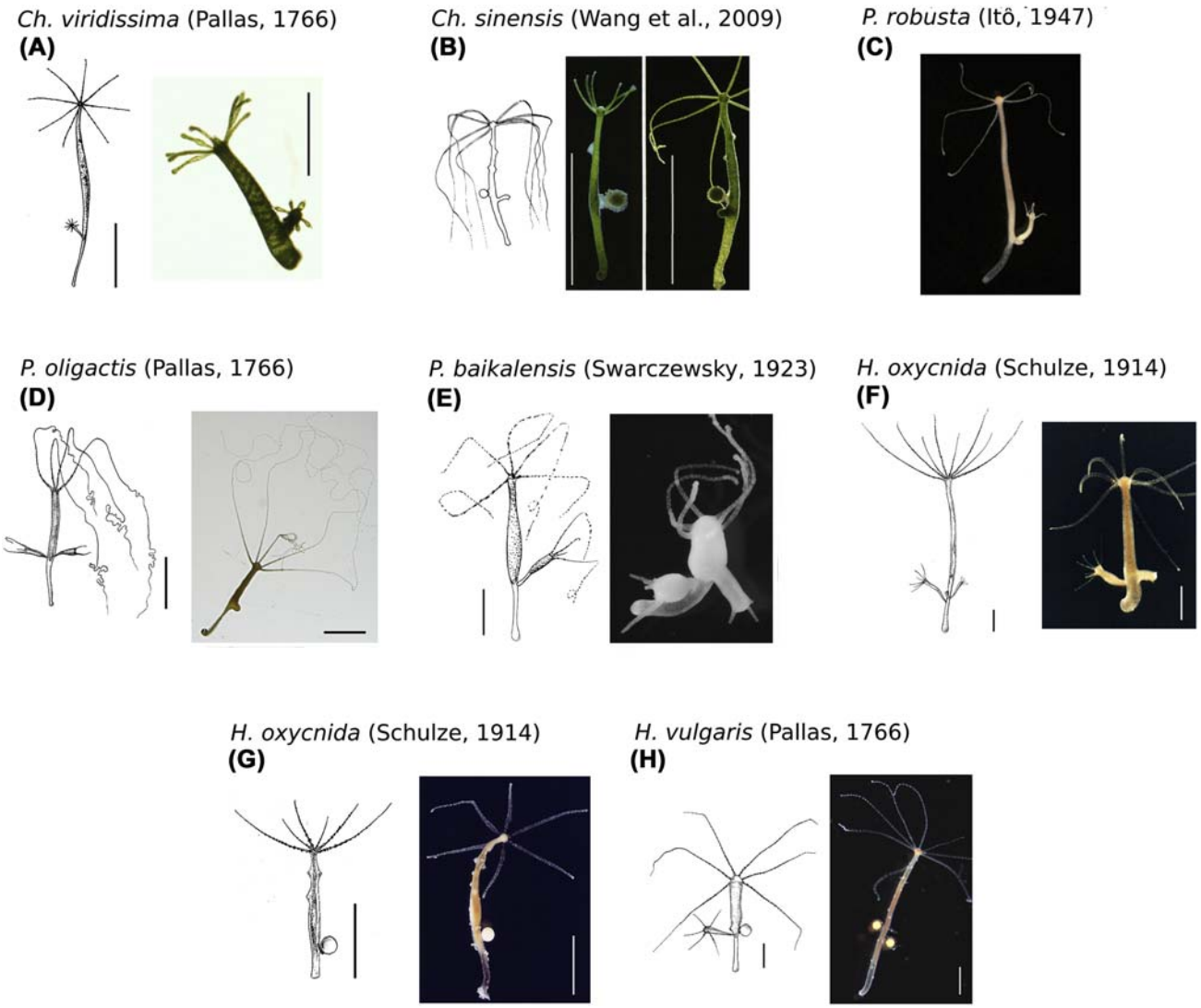


FIGURE 4.9 Habitus of different hydras species (B) Wang et al., 2009 (E) Anokhin, 2002. Scale Bars equal 3mm.

Hydrozoa: Moerisiidae: *Moerisia*: Species

Moerisia is a group of halophilic, mostly marine/brackish specimens. Some occur in salt lakes. Schuchert (2013) lists 10 *Moerisia* species. All except two are from outside the geographic range of this book or from marine habitats. In part, after Kramp, 1959, 1961.

1	Hydroids	2
1′	Medusae	3
2(1)	Hydranths appear to develop singly, with a length of over 2 mm; hydranth with a prominent distal cylindrical hypostome that is not constricted at its base; mouth opening surrounded by a narrow lip; basally the body tapers into a narrow stem; each hydranth bears a small number of long, filiform tentacles arranged in a circle around the broadest part of the body below the hypostome; number of hydranths is variable, and an individual may bear from 0–8 tentacles; the majority, however, possess 4 or 5 (according to Boulenger, 1908) (Fig. 4.3 G)	*Moerisia lyonsi* Boulenger, 1908 [Egypt. Introduced in Nearctic]

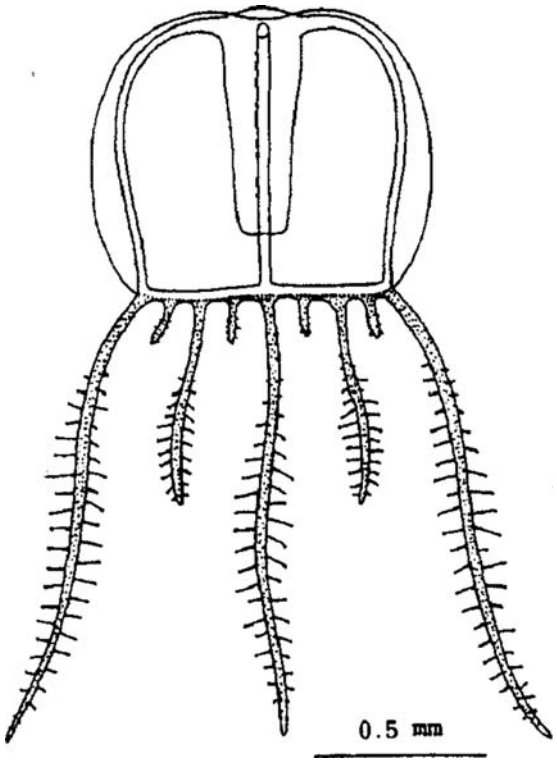


FIGURE 4.10 Habitus of *Astrohydra japonica* (Hashimoto, 1985).

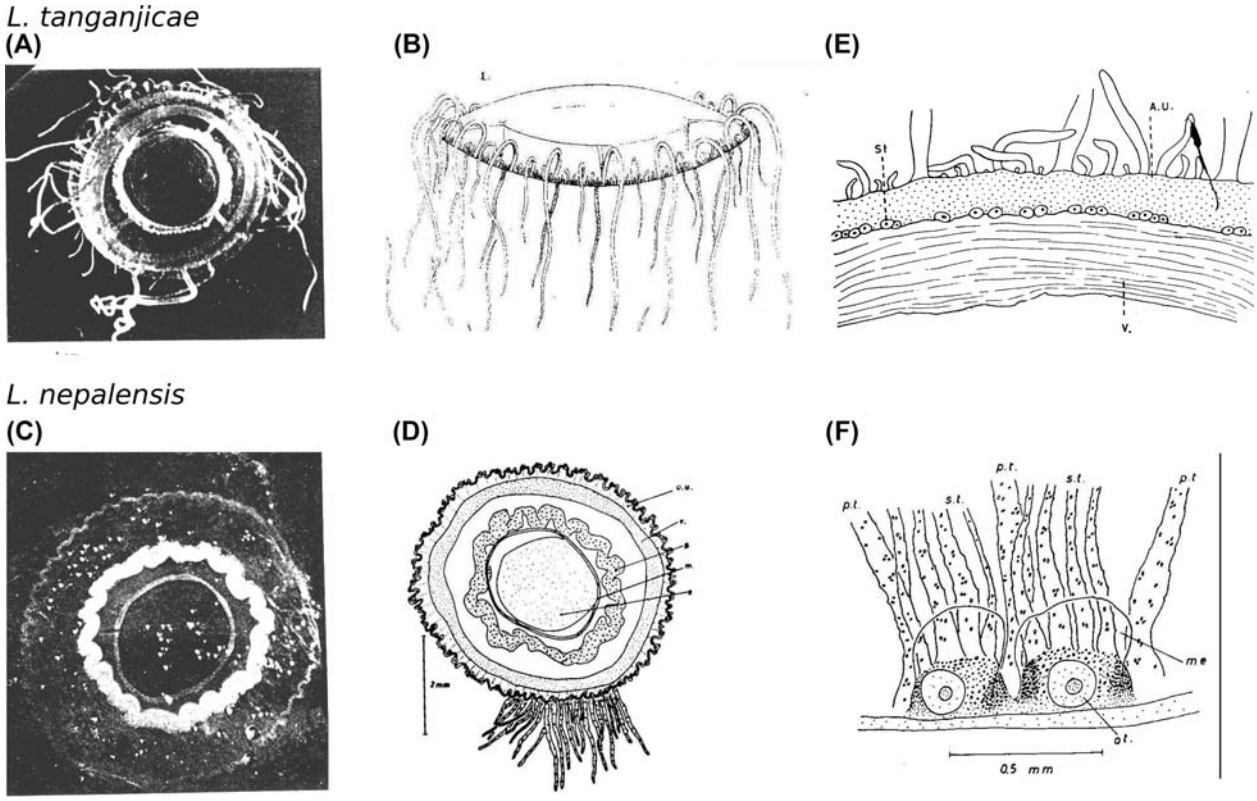


FIGURE 4.11 Habitus and umbrella margin of different *Limnocnida* species. *Modified from Jankowski, 2001 ((A and E) Bouillion, 1957, (B) Günther, 1893, (C, D, and F) Dumont, 1976).*

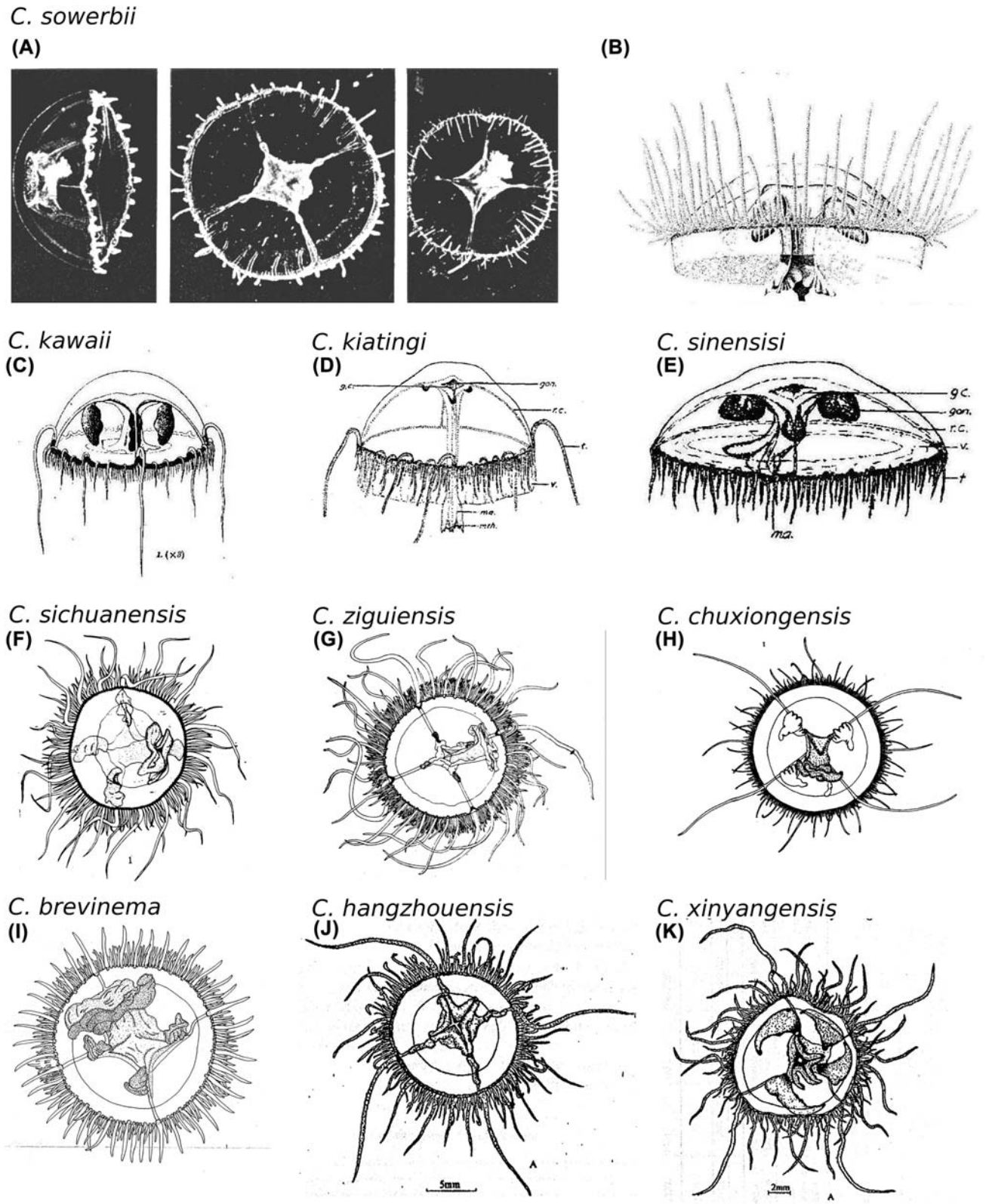


FIGURE 4.12 Habitus of different *Craspedacusta* species. *Modified form Jankowski 2001 (according to (A) Reisinger (1972), (B) Dejdar (1934), (Cc) Oka (1906), (D and E) Kramp (1951), (F) He & Kou (1984), (G) He & Xu (1985), (H) He et al. (2000), (I) He & Xu (2002), (J and K) He (2003).*

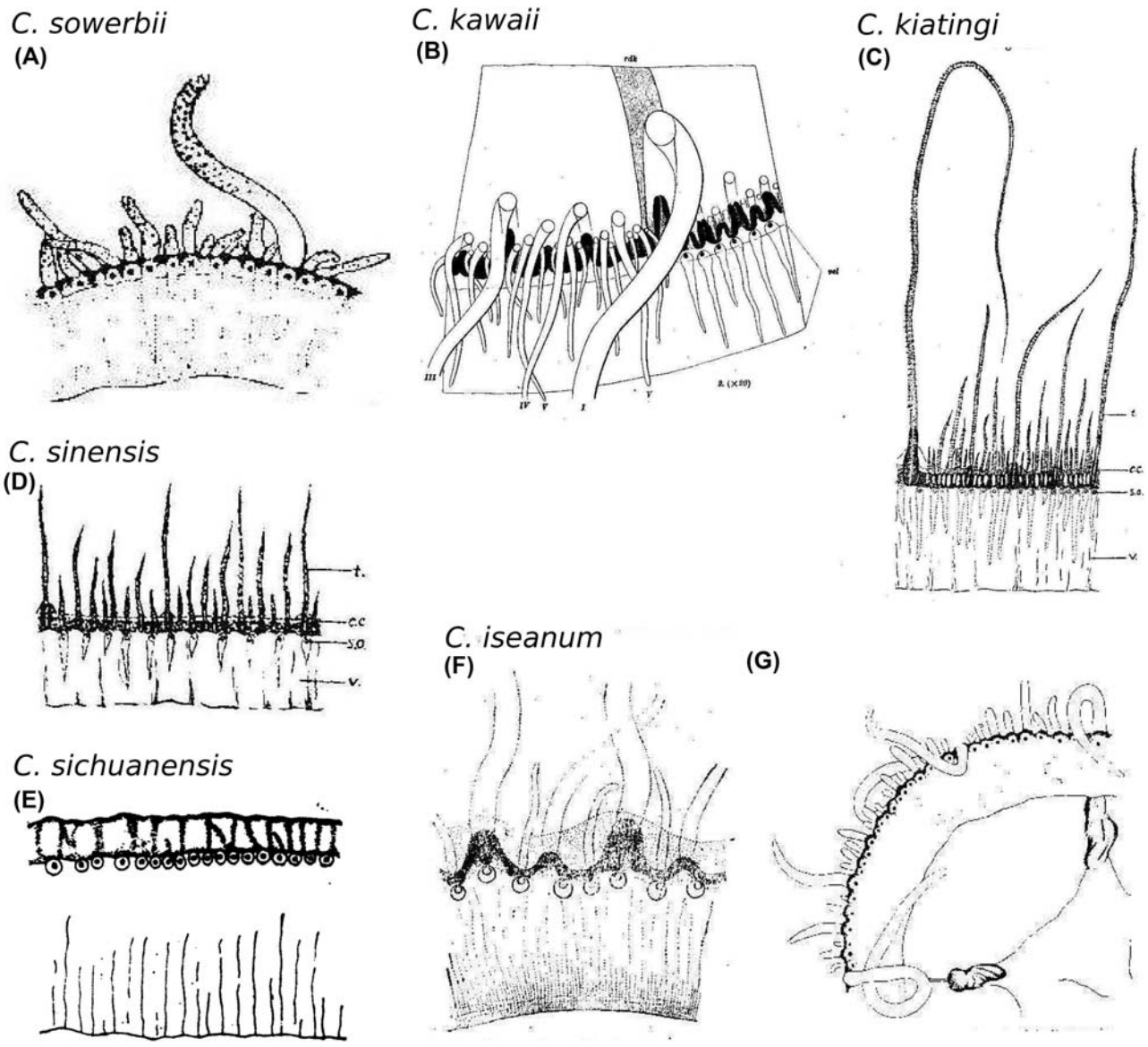


FIGURE 4.13 Umbrella margin with velum and statocysts of different *Craspedacusta* species. *Modified from Jankowski 2001 (according to (A) Uchida (1951), (B) Oka (1906), (C and D) Kramp 1951, (E) He & Kou (1984), (F) Uchida (1955), (G) Oka & Hara (1922).*

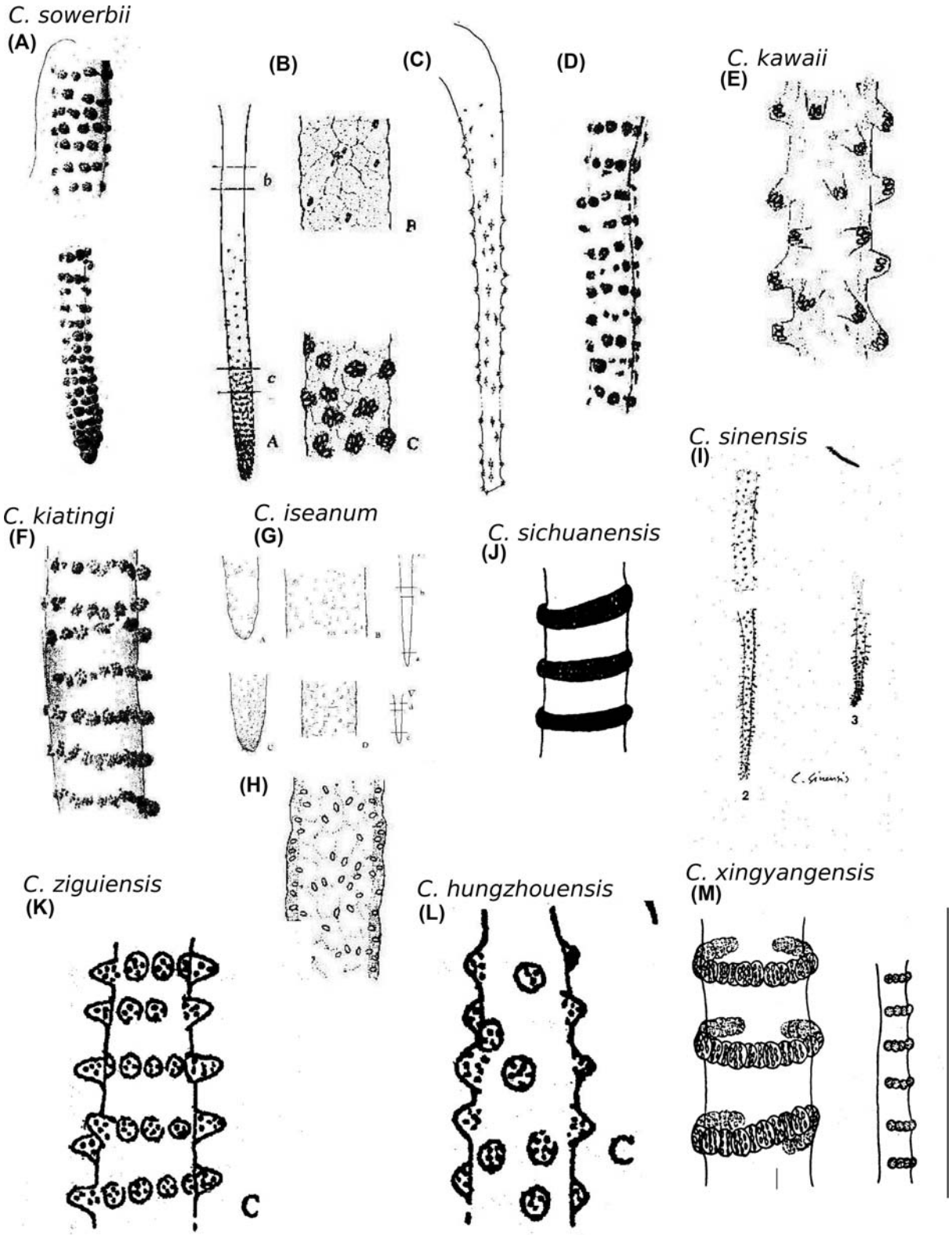


FIGURE 4.14 Tentacles and arrangement of nematocysts (and nematocyst warts) of different *Craspedacusta* species. *Modified from Jankowski 2001 ((A, D, F, and I) Kramp (1951), (B) Uchida (1951), (C) Dejdar (1934), (E and H) Oka & Hara (1922), (G) Uchida (1955), (J) He & Kou (1984), (K and L) redrawn from He (2003), (M) He & Xu (1985).*

2′ Hydranth length of over 1−1.5 mm.; colony reptant; hydrorhiza poorly developed in the form of small processes or filaments; perisarc very thin, covering only the hydrorhiza; polyp located on a thin stalk, body fusiform; hypostome conical, the mouth capable of opening very wide; each polyp bearing 7−15 simple filiform tentacles irregularly arranged; entire colony small, with no more than 5 or 6 zooids; solitary polyps also occurring; polyp body forming buds under the tentacles, with buds subsequently giving rise to medusae or polyps leaving the colony and leading a planktonic life (according to Naumov, 1960) ..... *Moerisia pallasi* Derzhavin, 1912 [Caspian Sea]

3(1) Medusa 4.5 mm wide, 4 mm high, globular, very thick; manubrium cylindrical, mouth round, without lips; radial lobes about two-thirds the length of the radial canals; tentacles usually four, sometimes 16, rarely up to 22, long, with prominent rings of nematocysts (Fig. 4.3 F) ..... *Moerisia lyonsi* Boulenger, 1908 [Egypt. Introduced in Nearctic]

3′ Medusa 3 mm wide, 3.5 mm high, convex, mesoglea thick; manubrium short, cruciform, mouth with four slightly indicated lips; radial lobes about two-thirds the length of the radial canals; up to 32 tentacles of different length in regular succession according to age (Fig. 4.3 H) ..... *Moerisia pallasi* Derzhavin, 1912 [Caspian Sea]

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Chapter 5

Phylum Platyhelminthes

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INTRODUCTION

The taxonomic group Turbellaria unifies the morphologically diverse free-living Platyhelminthes. This classification is based on their common acoel vermiform bauplan with bilateral symmetry. Most Turbellaria are small with a body size of around 1 mm, but some orders, such as Tricladida and Polycladida (marine flatworms not treated here), may range from 5 to10 cm. They are distributed globally and inhabit most aquatic environments. The sediments of marine, brackish, and fresh waters, as well as coral reefs, are suitable habitats along with open water or between the roots and leaves of aquatic plants.

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Turbellaria are considered one of the most basal bilateria (Littlewood & Bray, 2001) based on their archaic body structure. Nevertheless, Turbellaria are a very heterogeneous group of orders. Besides the overall body plan, most orders are "free living" (some groups are ectoparasitic, or endosymbiotic) and share some characteristic features of the body wall (simple epithelium, muscle network, absence of cuticle or dermal skeletal structures) and have regeneration based on stem cell-like neoblasts (Tyler & Hooge, 2004). These characters justified the grouping of the three main clades, Acoelomorpha, Catenulida, and Rhabditophora in the free-living Platyhelminthes, as Turbellaria (Tyler & Hooge, 2004). The Acoela and Nemertodermatida (Acoelomorpha) are treated as a phylum separate from Platyhelminthes, as they have dual spiral cleavage, bispiral segmentation, and an epithelium with a root system network (Ruiz-Trillo et al., 1999). This has been further supported by molecular studies (Ruiz-Trillo, 2002; Baguña et al., 2004a,b).

LIMITATIONS

The identification keys given below do not necessarily reflect the taxonomic relationships at phylogenetic or molecular levels (for this, see Egger et al., 2015). In order to achieve greater clarity, a simplified version of their relationships is used. It is therefore recommended that after identification, databases such as the Turbellaria Taxonomic Database (http://turbellaria.umaine.edu/turbella.php), Fauna Europaea (http://www.faunaeur.org), Erms (http://www.marbef.org/data/erms.php), WoRMS (http://www.marinespecies.org/), and EOL (http://eol.org/) be consulted. These are databases that combine specific information, distribution data, or essential bibliographic references.

TERMINOLOGY AND MORPHOLOGY

Important distinguishing criteria that are seen in living animals or through the "squash method" include the type and position of the pharynx, the organization of the reproduction organs, the presence or absence of eyes, pigmentation, and body shape. General important terms used for turbellarian determination in the keys are defined and explained following:

Adenal rhabdites: these structures are produced by gland cells near the epidermis (see rhabdites).

Adenodactyl: the auxiliary glandular bulb in male reproductive system of some groups, mainly Tricladida.

Adhesive glands: cell glands found in different parts of the body, which secrete adhesive substances.

Anterior ciliated pits: The ciliated pits or ciliated groves are paired and associated with the anterior cerebral lobes.

Ampullae or ampulla: vacuolated or glandular area of the proboscis of some Kalyptorhynchia.

Ascus: glandular pocket near the genital pore. The ascus is characteristic for Ascophorinae, and their function is related to reproduction, but is incompletely known.

Atrium copulatorium: the space into which bursa copulatrix and male copulatory organ open; usually separated by a sphincter from the female reproductive system.

Atrium genitale communis: the space into which both the male and female systems open. They can be present in different shapes and development: (1) simple, (2) differentiated as superior and inferior, (3) with a diverticulum or blind sac, (4) with a sphincter between atria, (5) with a double sphincter between atria, (6) with a double or single sphincter in the genital pore, (7) with a diverticulum with spines, or (8) differentiated in male and female genital atrium.

Body shape: Turbellarians show various body shapes: (1) fusiform with rounded anterior end and posterior end blunt pointed, (2) fusiform with anterior and posterior end blunt pointed, (3) elongated, anterior and posterior end rounded, with ciliated furrow or with anterior end developed as prostomium, (4) anterior end slight pointed, posterior end rounded, (5) anterior truncated, posterior rounded, (6) anterior truncated with "ears," posterior end rounded, (7) fusiform with tapered or rounded anterior end and posterior end blunt pointed, or (8) anterior and posterior end rounded.

Brain: the main ganglion or brain shows different shapes: (1) ovoid without anterior lobes, or (2) ovoid with anterior multilobes.

Bursa copulatrix: part of the reproductive system into which sperm are deposited, very variable in development and shape. Usually opening into the genital atrium. They can appear: (1) without stalk, (2) with stalk, (3) saclike with a broad stalk, (4) paired (two bursa copulatrix), or (5) absent.

Chain of zooids: usually the presence of zooids numbers two or three, but sometimes some species can contain two or more (multiple) zooids.

Coloration: the pigmentation within the flatworm is variable, depending mainly on the intestinal or parenchymal content: (1) translucent whitish, (2) translucent with spots and dots, (3) dark pigmentation at the dorsal

side, (4) dark pigmentation (reddish or brownish) at the dorsal and ventral side, (5) translucent yellow to brown or green (through gut or parenchyma content), (6) translucent gray-yellow, or (7) whitish opaque.

Ciliated pits: Sensory structures (e.g., anterior end of Stenostomidae).

Copulatory organ: Bulbous organ that contains the sperm duct and elements of the prostate system. When not armed with hard structures, yet capable of protrusion, it is simply called a penis papilla. It may be enclosed in a small inner chamber (penis pocket) the wall of which can form a small prominence (penis sheath). One or more hard structures in the copulatory organ constitute a sclerotized apparatus like a stylet or a spiny cirrus. The male copulatory organ can be of different shapes: (1) retort shaped (rounded copulatory organ with a curved penis papilla), (2) pyriform, elongated, (3) elongated, (4) oval, or (5) anchor-shaped. Likewise, the position in respect the main body axes can be present different orientations of taxonomical importance: (1) frontal oriented, (2) caudal oriented, or (3) ventral oriented.

Dermal or epidermal rhabdites: present/absent. Dermal rhabdites are produced by specific, epidermal cells.

Ducto genito-intestinalis: duct or canal between the female system and the intestine, may be present or absent.

Ductus ejaculatorius: terminal canal of the male copulatory organ, sometimes eversible, sometimes sclerotized or with spines; it carries the reproductions secretions. The different shapes and natures of the ejaculatory duct can be resumed as following: (1) not sclerotized, muscular, (2) sclerotized, (3) pseudosclerotized, (4) cirrus with spines, (5) with stylet, or (6) muscular with an accessory bag and sclerotized sheets.

Ductus spermaticus: duct through which sperm reach the female system (the receptaculum seminis or the ductus communis). They can be present or absent.

Excretophore: Large vacuolated cells of the intestine epithelium.

Eyes: light-sensitive structures mostly near the brain and with different shapes and development as follow: (1) reniform without anastomosis, (2) strongly reniform marked with smooth bridges between the anterior and posterior units of the single eyes, (3) with anastomosis, (4) crescentiform without anastomosis, (5) rounded without anastomosis, (6) present diffuse, (7) triangular, reddish, or (8) absent.

Granular or prostatic secretion: secretions of the male reproductive system, free into the male copulatory bulb, near the seminal vesicle, or enclosed in a distinct vesicle, the prostatic vesicle or vesicle granulorum. These vesicles are sometimes combined with the seminal vesicle within the male organ or separate as a proper organ. In summary, the prostatic secretion can be: (1) free, laterally and next to the vesicula seminalis (vesicula granulorum or prostatic vesicle absent), (2) free, distal to the vesicula seminalis (vesicula granulorum absent), (3) free, but with lobes bunched, (4) free, but in a reservoir, or (5) in a true vesicula granulorum or prostatic vesicle.

Gut with excretophores: in some orders of Platyhelminthes like the Catenulida the gut can show large vacuolated cells near or within the gut walls, the excretophores.

Location of male pore: in relationship to the oral pore can be before, behind, or dorsal at level of the oral pore.

Main excretory ducts opening: osmoregulatory and excretion system of the Platyhelminthes. The opening of the main trunks of the excretion system is variable within the distinct families and genera. In summary: (1) separated on body wall, (2) separated in the pharynx pouch, (3) separated and just in front of the genital pore, (4) together in the pharynx pouch, (5) together in a posterior pouch, (6) in a pharyngeal excretory pouch, (7) through a common pore between oral and genital pores, or (8) unpaired, open in front of the pharynx.

Opening of the prostatic glands into the prostatic vesicle: The prostatic glands can open in distinct ways into prostatic vesicle: (1) proximally, together with the vas deferens, (2) proximally, but separated from the vas deferens, (3) laterally, mid-proximal region, (4) laterally, mid-distal region of the copulatory organ, (5) internally, prostatic glands located between the male muscular layers, (6) proximal into the vesicula granulorum, or (7) unknown.

Oral and genital pore: may be variously located, either common or separated, but in the same body third, or well separated, in different body thirds.

Ovary: the female gonad. The orientation of the ovary can be caudal or frontal. Also, at the genus level, the ovary is either paired or unpaired, but always separated from the vitellaria. Sometimes the vitellaria and ovary appear together and forms the ovovitellaria.

Penis papilla: the penis papilla is the terminal part of the male system devoid of rigid structures like a stylet or spines. The penis papilla can show distinct shapes and sizes: (1) short and small, (2) conical and well developed, or (3) absent.

Pharynx: there are different pharynx types: (1) cylindrical (doliiformis), (2) rosulatus, (3) tubular or plicate, or (4) simple. The pharynx is a glandular-muscular structure embedded in the digestive system and has high taxonomic value. The pharynx location within the body organization is

variable: (1) anterior (in the first body half), (2) posterior (in the last body half), or (3) central (between the first and the last body halves).

Vaginal pore: female opening ventral or dorsal located and separate from the female pore.

Prepharyngeal organ or pit: the prepharyngeal organ is a ventromedial diverticula with numerous cyanophilic glands, located shortly before the pharynx and characteristic of ***Bothromesostoma*** (Mesosominae). The prepharyngeal organ opens to the exterior through a small ciliated grove or epidermal fold, the prepharyngeal pit.

Proboscis: anterior muscular organ characteristic of the Kalyptorhynchia. Depending on the subtaxa (Polycystide, Karchinorhynchidae, etc.), the proboscis is split and can present hooks and spines.

Prostatic vesicle: part of the male reproductive system. The structure containing gland cells, and its secretions are combined with the sperm outside the body during their release.

Prostomium. Body region anterior to mouth; usually containing the brain.

Receptaculum seminis: it is part of the female apparatus, located between the germarium and the ductus communis (female canal) and is used for storing of sperm. The shape and localization of the receptaculum seminis is variable: (1) present with stalk, (2) present without stalk, (3) in the germiduct included, or (4) absent.

Retractable anterior end: The anterior part can be very mobile in Typhloplanidae. Sometimes this region can be retracted and projected almost telescopically (as in Rhynchomesostoma).

Rhabdites: adenal and dermal inclusions secreted by glands often concentrated as rods at the anterior end of the body (Rhabdite rods). The function of these secretions is not well known, apparently these structures are related with the defense.

Spines: sclerotized structures, which are present mainly in the male copulatory organ or in the bursa copulatrix/atrium copulatorium.

Statocysts: orientation organ consisting of sensory cells that surround a statolith (granule).

Stylet: the stylet is one of the most variable structures within the reproductive system: (1) funnel-like and curved, (2) funnel-like, straight with curved end, (3) straight (aciculate or angular), (4) curved, sinuate, (5) curved, spiniform, (6) retort-like, (7) with two handles and spines (separated in ***Fulinskiella***), (8) with two handles, central channel and spines, (9) with one handle and spines, (10) with girdle and spines, (11) a double stylet composed of a bridge with spines with an accessory cuticular structure, or (12) simply absent. Likewise the spines show multiple combinations: (1) same shape and size, homogeneous spines (in ***Varsoviella*** both lateral spines hamulate), (2) distinct shape and size, heterogeneous spines, (3) with different or same shape and size, (4) with one individual accessory spine near the stylet, or (5) spines absent.

Testes: male organs for sperm production. The testes are paired compact organs with different shapes and positions: (1) elongated or clavate, (2) follicles-chains, (3) clavate anteriorly, in front or next to the pharynx, (4) clavate anteriorly end, just behind the pharynx, (5) clavate, at the posterior body half, next or behind the copulatory organ, (6) clavate next or behind the pharynx, or (7) unpaired elongated organ. With respect to the vitellaria, the location varies between the different taxa: (1) ventral to the vitellaria, (2) dorsal to the vitellaria, or (3) in front of the vitellaria.

Uteri: part of the female apparatus where eggs are stored. The sack-shaped uteri are paired or unpaired and open into the ventrolateral wall of the genital atrium. They can be: (1) paired H-shaped, (2) paired U-shaped, (3) paired T-shaped, (4) unpaired, (5) unpaired with a sphincter, or (6) absent (egg stored in the atrium genitale or distal end of the ductus communis).

Vasa deferentia: Vasa deferentia are main collecting ducts that run from testes to male copulatory structures, and the opening can be: (1) separated, lateral and caudally into the copulatory organ, (2) separated at the proximal end of the copulatory organ, (3) together, through a common vas deferens, or (4) together at the proximal end. The shape of the ducts can be: (1) tubular without dilatations, (2) tubular with dilatations (external or false vesicula seminalis), or (3) tubular with dilatations (sperm vesicles or bulbs).

Vesicula seminalis: The distal end of the vasa deferentia expands into a spherical bladder, the seminal vesicle or vesicula seminalis, which is used for sperm storage and is either rounded or elongated or absent.

Vitellaria: or yolk glands may be of distinct shapes and sizes: (1) smooth tubes, (2) smooth tubes that meet anteriorly behind the pharynx, (3) unpaired smooth tube, (4) unpaired and branched, (5) paired lobular, (6) paired follicular, (7) paired plumiform, or (8) absent as proper organ, together with the ovary (ovovitellar).

Zoochlorellae: may be absent or present.

ABBREVIATIONS USED IN FIGURES

ac atrium copulatorium
as accessory spine (thorn)
asc ascus
atg atrium genitale communis

b brain
bc bursa copulatrix
bg brain ganglia
bs blind sac
c cirrus
cf ciliated furrow
cip ciliated pits
cm circular muscle
cm circular muscles
co copulatory organ
dc ductus communis
de dusctus ejaculatorius
dfp dorsal female pore
ds ductus espermaticus
e eyes
eg egg
esv external seminal vesicle
ex excretophores
fa female atrium
fg frontal glands
fo frontal organ
fp female pore
g glands
gp genital pore
h hooks
i intestine
ib intestinal bursa
inc inclusions
m muscle
med main excretory ducts
mp male pore
op oral porus
ov ovary
ovd oviduct
p pigmentation
pb penis bulb
pg prostatic glands
ph pharynx
phg pharyngeal glands
pp penis papellae
ppho prepharyngeal organ
pr proboscide
ps prostatic secretions
pt prostomium
pv prostatic vesicle
rb rhabdites
rbg rhabdite glands
rbr rhabdite rods
ro refractil organs
rs receptaculum seminis
sc spiny cirrus
shg shell glands
sb sperm bulb
sp spines
sph sphincter
st stylet
stc statocyste
sv seminal vesicle
t testes
th thorn
u uterus
v vitellaria
vd vas deferens
vfp ventral female pore
vid vitelloduct
w warts
z zooids

MATERIAL PREPARATION AND PRESERVATION

Most freshwater turbellarians are small and delicate, and therefore a hand net is necessary. The hand net should be dragged carefully through the vegetation or the water surface. The contents must be removed and deposited in a suitable container. Collection bottles or similar container can be used as an improvised dredge to collect sediment samples from the bottom of rivers or ponds. Specimens should not be fixed or preserved in the field. The worms must be observed first live in the laboratory before being fixed.

In the laboratory the animals should be removed from the sample debris and studied under stereomicroscopes. Notes about the size, shape, and movement of the animal must be taken. Those specimens that are transparent or very small can still be observed under the microscope using a slide and a cover slip in order to squash them slightly and study the internal organization. Most have to be fixed in Bouin's or 5% formaldehyde for histology. Obtaining serial sections (4–8 microns depending on size) allows us to reconstruct the internal organization of the reproductive apparatus and to complete the determination.

The animals that will not be directly processed can be stored in 70% alcohol. With few exceptions, the characters used in the following keys are viewable by transparency ("squash method") (Figs. 5.1–5.15).

KEYS TO PLATYHELMINTHES

Platyhelminthes: Orders

1	Eyes mainly present	2
1′	Eyes mainly absent	5
2(1)	Pharynx plicatus or variabilis; testes follicular; stylet absent	3
2′	Pharynx another type; testes paired; stylet present	4
3(2)	Brain ovoid without lobes; Ciliated pits present; sclerotic male structures absent; statocyst absent	**Tricladida**
3′	Brain with anterior and posterior lobes or trunks; ciliated pits absent; sclerotic male structures present; statocyst present	**Proseriata**
4(2)	Ciliated pits absent; pharynx doliiformis or rosulatus; sexual reproduction present, asexual absent; cirrus, stylet, or spines present	**Rhabdocoela**
4′	Ciliated pits present; pharynx another type; asexual and sexual reproduction present; stylet present, cirrus absent	**Macrostomida**
5(1)	Stylet present and/or sclerotic male structures present	6
5′	Stylet absent; sclerotic male structures absent	7
6(5)	Pharynx plicatus (tube-shaped) or variabilis; brain ovoid without lobes; oral and genital pore common, usually at the anterior end; ciliated pits absent	Lecithoepitheliata, one family; **Prorhynchidae**
6′	Pharynx simplex; brain with anterior and posterior lobes and trunks; oral and genital pores separated; ciliated pits or statocyst present	**Catenulida**
7(5)	Brain ovoid without lobes; ciliated pits absent; testes follicular; coloration: pigmented	**Prolecithophora**
7′	Brain with anterior and posterior lobes or trunks; ciliated pits present; testes paired; pigment less; (Fig. 5.15 I)	Bothrioplanida: Bothrioplanidae, one species: *Bothrioplana semperi* Braun, 1885

Platyhelminthes: Tricladida: Families

1	Usually unpigmented, whitish opaque	2
1′	Usually pigmented (dark or beige)	3
2(1)	Anterior body end truncated, with tentacles reduced to prominent edges; with (one pair or multiple) eyes or without eyes; usually unpigmented; adhesive disc absent; inner muscular layers of the pharynx with crossed longitudinal and circular muscles layers; with or without adenodactyls	**Dendrocoelidae**
2′	Anterior body shape pointed, posteriorly widen rounded, bottle-like; without tentacles; one pair rounded eyes if present; pigmentation whitish; adhesive disc present; one median and two lateral gonopores ventrally; usually with an intrapenial papilla, two lateral bursae, and ventral or dorsoventral testes (after Sluys, 1989); mainly marine	Bdellouridae, one species: *Pentacoelum fucoideum* Westblad, 1935 [Caspian Sea]
3(1)	Anterior body rounded; pointed tentacles present in some genera; multiple eyes around the anterior margin or only one pair bean-like or without eyes; adhesive disc absent; muscle layer of the pharynx inner circular and the outer longitudinal	**Planariidae**
3′	Anterior body shape triangular; pointed tentacles absent; one pair eyes, sometimes surrounded by a unpigmented circular area; pigmentation dark to whitish; adhesive disc absent; oviducts run separately and open at the end of bursa copulatrix	**Dugesidae**

Platyhelminthes: Tricladida: Dendrocoelidae: Genera

Body elongate, anterior region truncated with rounded and slightly outstanding edges, posterior rounded. Coloration translucent, light pigmented or whitish. With anterior adhesive organ. Without posterior adhesive disc. With or without one pair eyes. Pharynx with interleaved circular and longitudinal muscular layers. Oviducts open combined into the atrium. Spermiducal bulbs present. Penis papillae conical and short. With glandulomuscular organ or adenodactyls. Shell glands open into the common oviduct.

1	Tricladida without adenodactyls in reproductive system	2
1′	Tricladida with adenodactyls	18
2(1)	Eyes present	3
2′	Eyes absent	16
3(2)	Eyes paired	4
3′	Numerous eyes in clusters	10
4(3)	One pair of eyes	5
4′	Two or three pairs of eyes	8
5(4)	With whitish eyes fields, body margins, or transverse bands behind the paired eyes	6

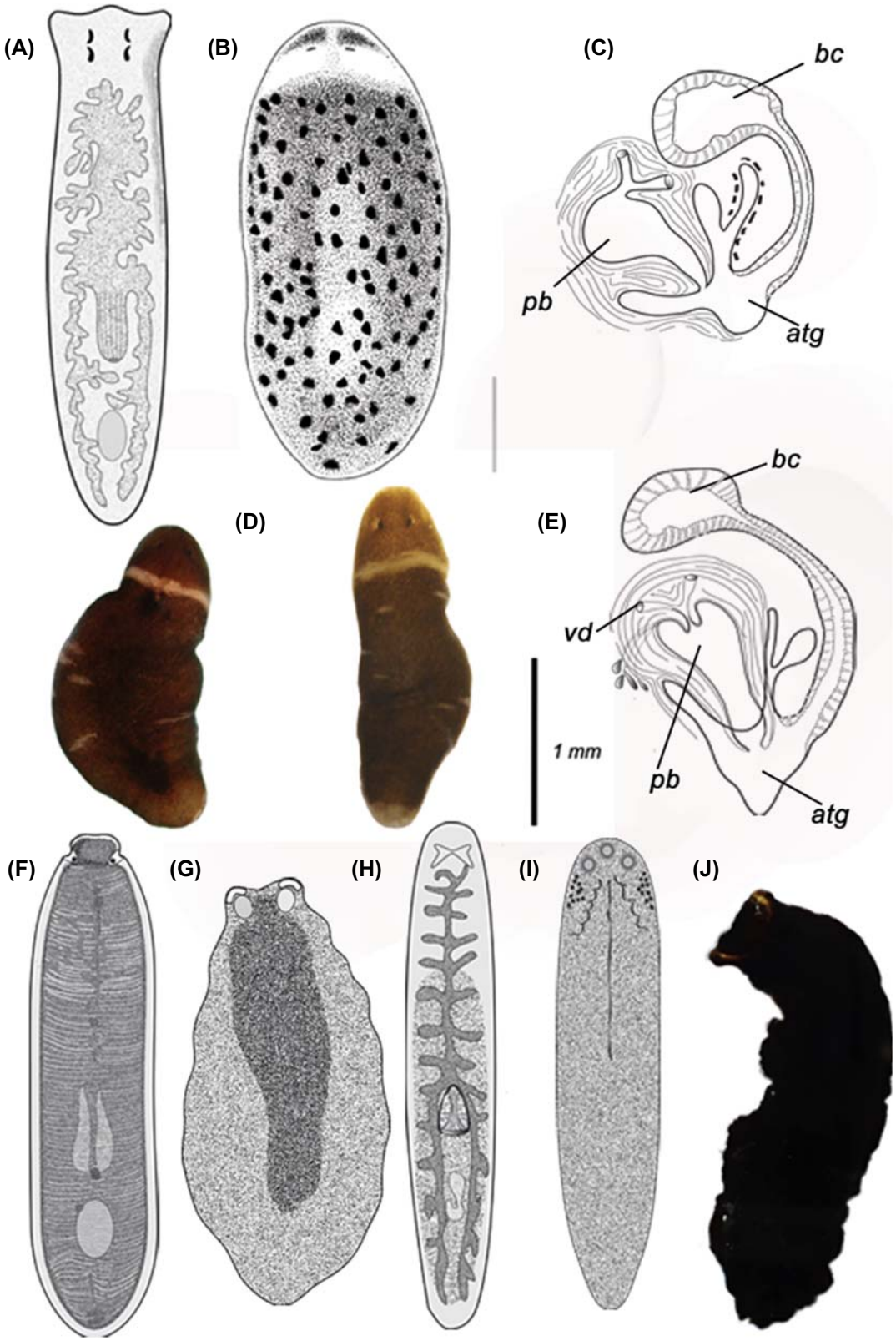


FIGURE 5.1 Dendrocoelidae, Tricladida: (A) *Dendrocoelopsis*; (B) *Vermipharyngiella*; (C) Reproductory organs; (D) *Microarchicotylus*; (E) Reproductory organ; (F) *Bdellocephala*; (G) *Papilloplana;* (H) *Miodendrocoelum;* (I) *Protocoylus;* and (J) *Hyperpapillina*.

5′	Without whitish bands or fields, pigmentation usually irregular 9
6(5)	Without transverse bands 7
6′	With a transverse band behind the eyes; body and anterior end elongate with a blunt head; penis papilla elongate; shell glands open into the bursa stalk; copulatory organ compact and located behind the pharynx, apical part directed downwards; bursa copulatrix, canal of bursa, male and common atrium asymmetrical with respect to medial longitudinal body axis and gonopore; (Figs. 5.1 D, E) ..... *Microarchicotylus*
7(6)	Body and anterior end elongated and with a head markedly narrower as the rest of the body; penis papilla conical, short; anterior body truncated and with prominent edges; shell glands open into the common oviduct; (Fig. 5.1 F) ..... *Bdellocephala*
7′	Body oval, eyes arranged in groups (6−15) in a whitish field; on the dorsal side can be papillae, like tubercles; small forms; (Fig. 5.1 G) ..... *Papilloplana*
8(4)	Pigmentation light brown; adhesive disc present; penis papilla conical short; papilla cells with crystalloid; (Fig. 5.2 G) ..... *Armilla*
8′	With coloration not as above, generally lightly pigmented; adhesive disc present; penis papilla elongated; (Fig. 5.2 F) ..... *Archicotylus*
9(5)	Coloration milky-white or lightly pigmented; tentacles absent; adhesive disc absent; (Fig. 5.1 H) ..... *Miodendrocoelum*
9′	Pigmented dark spots on a light background; wall of pharyngeal canal with three well separated, compactly arranged muscular layers: subepithelial circular, medial longitudinal, and inner circular; bursa copulatrix with crystalloids; (Figs. 5.1 B, C) .... *Vermipharyngiella*
10(3)	Numerous eyes arranged in groups 11
10′	Numerous eyes arranged in two parallel rods, tentacles reduced to conspicuous edges; (Fig. 5.1 A) ..... *Dendrocoelopsis*
11(10)	Body and anterior end elongate with blunt head not markedly narrowing 12
11′	Body and anterior end elongated and with a head markedly narrower than the rest of the body 15
12(11)	Penis papilla inerm 13
12′	Penis papilla with hard structures or cover 14
13(12)	Eyes inconspicuous, grouped; tentacles present as incipient tentacles or reduced to prominent edges; adhesive disc present; dark pigmented; penis papilla long and thick with basement membrane; (Fig. 5.1 J) ..... *Hyperpapillina*
13′	Eyes numerous, arranged in several groups or rows; some species with reduced tentacles or prominent edges; adhesive disc present; pigmentation sandy (dark or light); penis papilla with a well-developed dorsal lip; (Figs. 5.2 A, B) ..... *Sorocelis*
14(12)	Eyes arranged in two groups; adhesive disc or discs present; penis papilla conical, short covered with spiniform structures; (Fig. 5.1 I) ..... *Protocotylus*
14′	Eyes very difficult to distinguish, usually simple pigment accumulations on the upper surface; penis papilla with collagen cover; ductus ejaculatorius with long nipples; pigmented; (Fig. 5.2 C) ..... *Alaoplana*
15(11)	Pigmentation uniformly dark or light brown with dark spots; (Fig. 5.2 D) ..... *Rimacephalus*
15′	Pigmentation light with dark crosswise strokes; reproductive system with large atrium genitale communis; (Fig. 5.2 E) ..... *Baikalocotylus*
16(2)	Without adhesive disc 17
16′	With numerous adhesive discs or suckers (over 100) along body margin; form very large, length 15 cm; (Fig. 5.3 A) ..... *Baikaloplana*
17(16)	Pigmentation dark (marine species whitish); penis bulb with multiple muscle layers (40), penis papilla elongated with collagen cover; tentacles absent; glandular field present; (Fig. 5.2 H) ..... *Hyperbulbina*
17′	Pigmentation light brown; penis papilla conical, short; tentacles present as incipient tentacles or reduced to simple edges; glandular field absent, without bursa copulatrix; (Fig. 5.2 I) ..... *Atria*
18(1)	Adhesive disc absent 19
18′	Adhesive disc present 20
19(18)	One adenodactyl; wall of pharyngeal canal with two muscular layers: subepithelial longitudinal and inner circular; (Fig. 5.3 B) ..... *Caspioplana*
19′	Several adenodactyls (1−9); numerous eyes on inner side of oval white fields; pigmented; with a broad body and a slightly triangular head; (Fig. 5.3 F) ..... *Baikalobia*
20(18)	Numerous eyes 21
20′	Eyes of two pairs or absent; tentacles present as incipient tentacles or reduced to prominent edges; anterior body truncated, pigmentation usually whitish or translucent; (Fig. 5.3 C) ..... *Dendrocoelum*
21(20)	Eyes arranged in two parallel arcs; tentacles reduced to prominent edges or absent; adenodactyl connected to the common atrium by long and thin duct; bursa copulatrix replaced by genito-intestinal ducts; (Fig. 5.3 D) ..... *Acromyadenium maroccanum* de Beauchamp, 1931
21′	Eyes arranged in groups or absent; tentacles reduced to prominent edges or frequently absent; adenodactyl well developed, sometimes larger as male copulatory organ; (Fig. 5.3 E) ..... *Polycladodes*

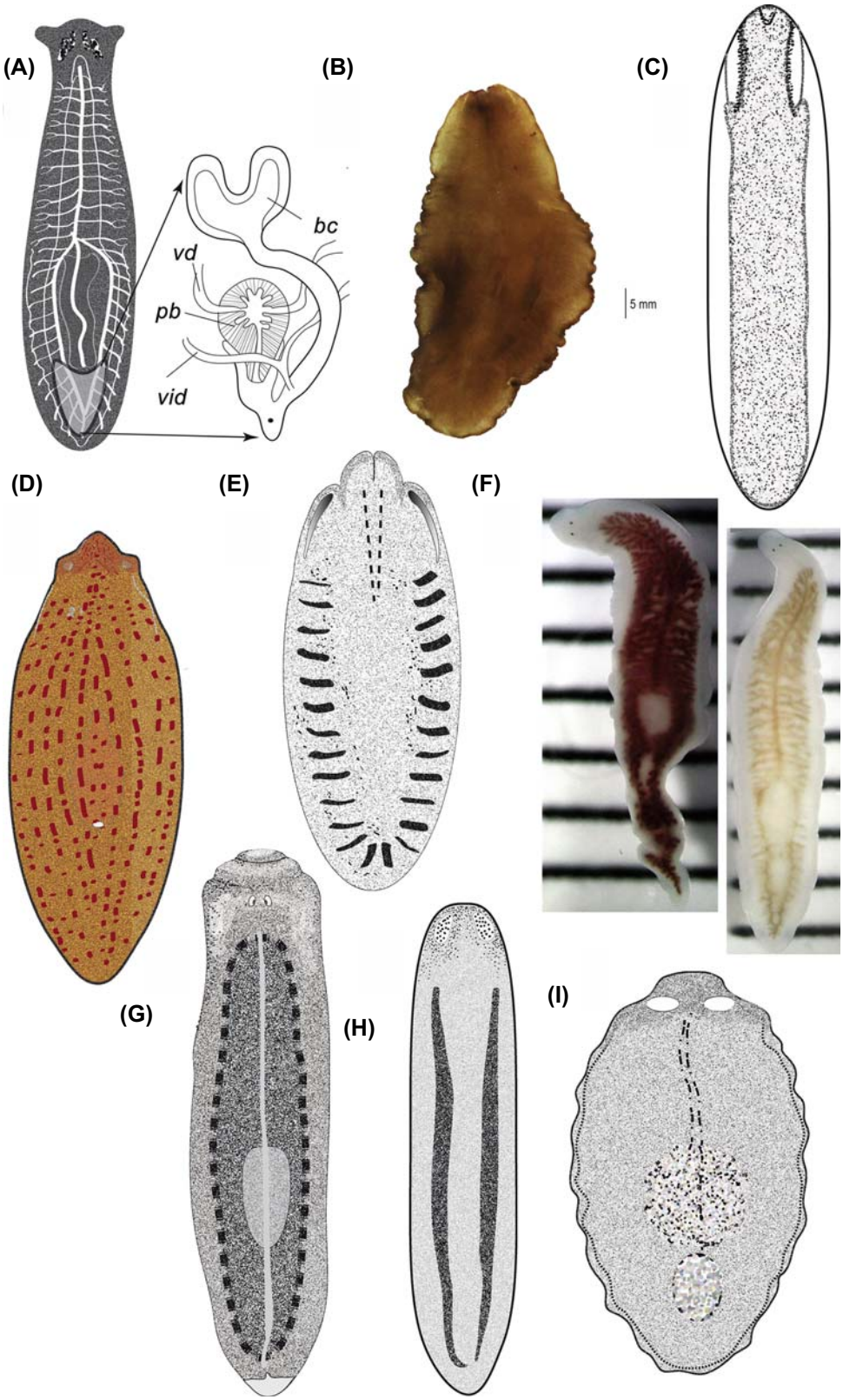


FIGURE 5.2 Dendrocoelidae, Tricladida: (A) *Sorocelis*; (B) Photo *Sorocelis*; (C) *Alaoplana*; (D) *Rimacephalus*; (E) *Baikalocotylus*; (F) *Archicotylus*; (G) *Armilla*; (H) *Procotyla*; (I) *Hyperbulina*; and (J) *Atria*.

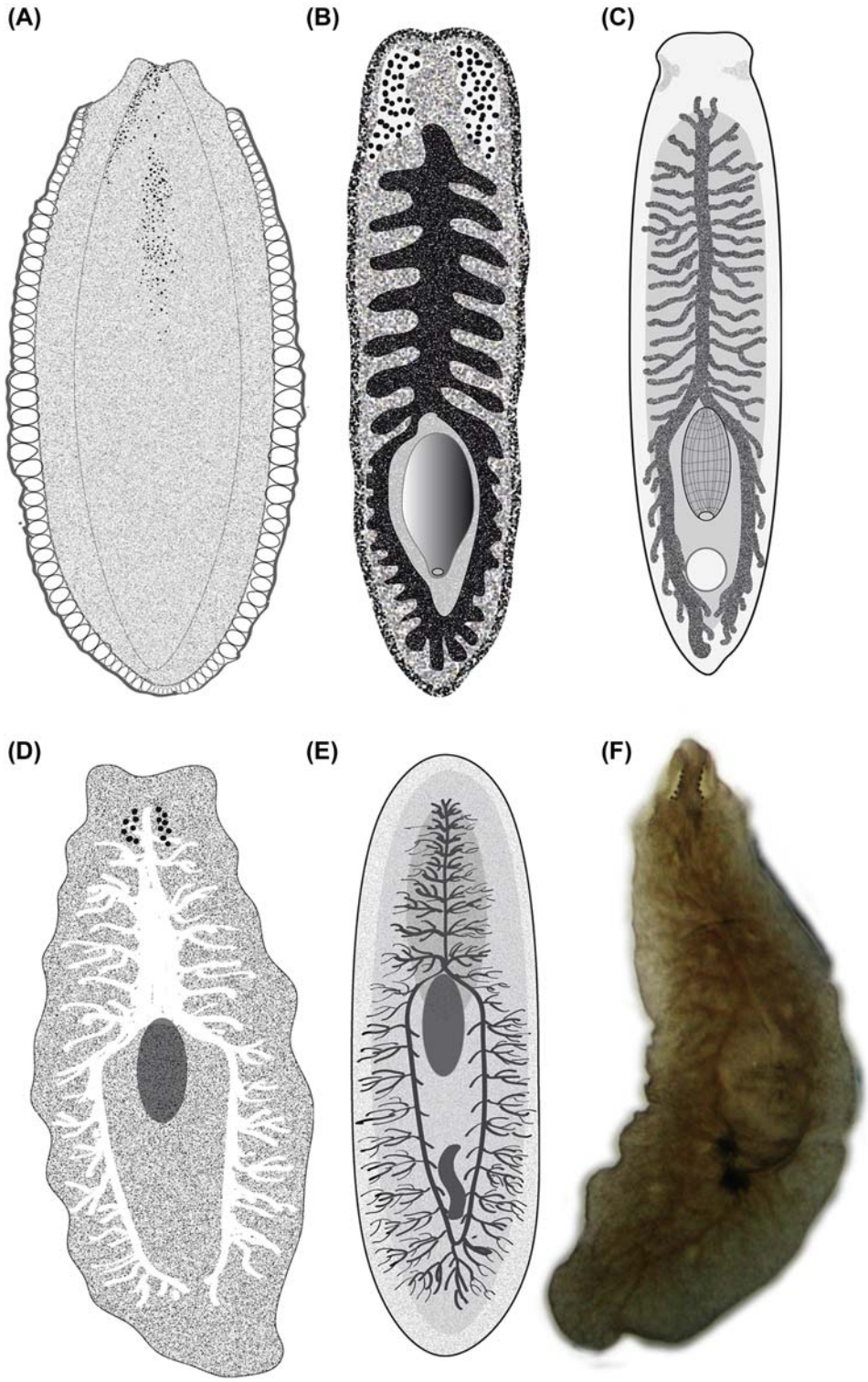


FIGURE 5.3 Dendrocoelidae, Tricladida: (A) *Baikaloplana*; (B) *Caspioplana*; (C) *Dendrocoelum*; (D) *Acromyadenium*; (E) *Polycladodes*; and (F) *Baicalobia*.

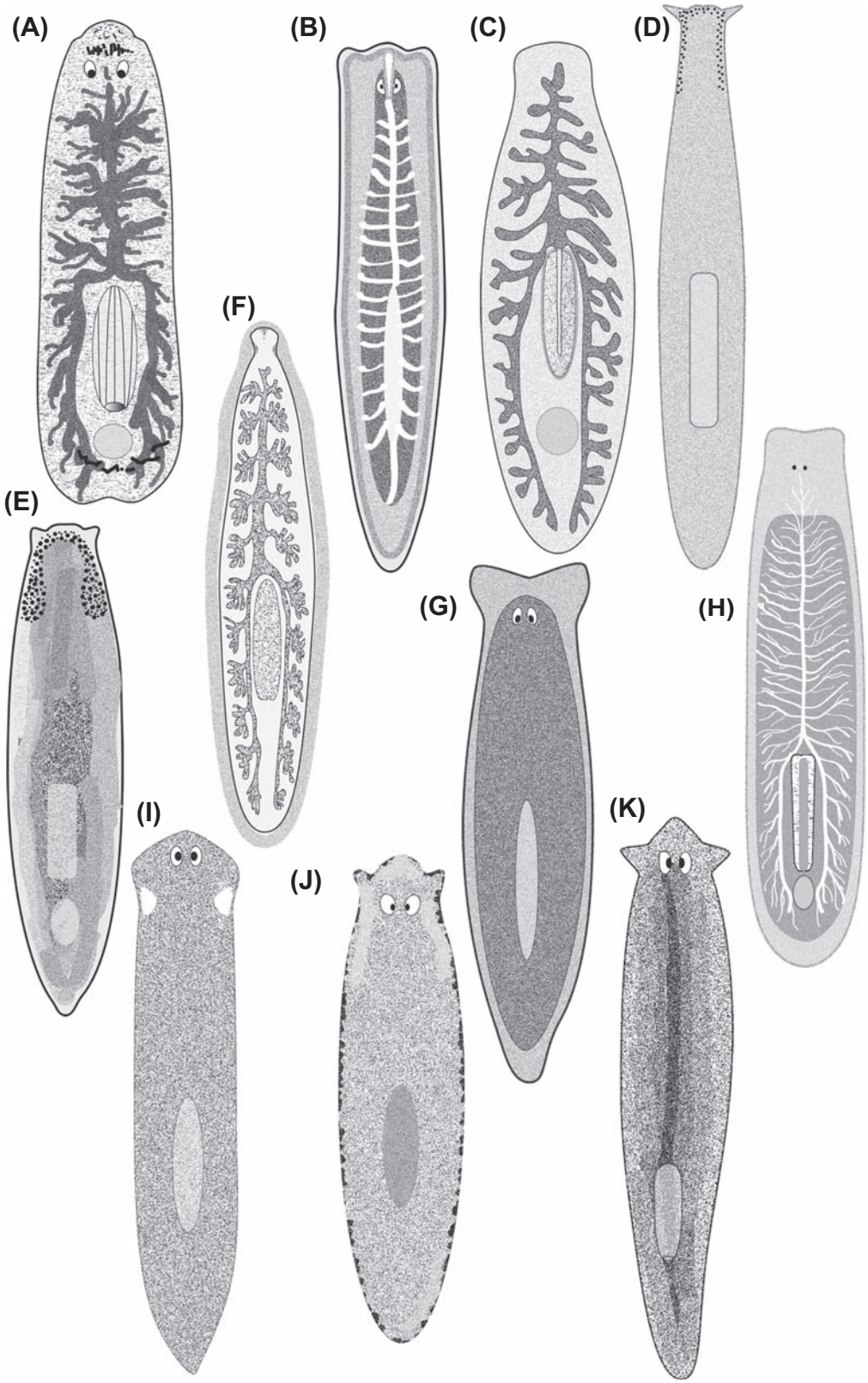


FIGURE 5.4 Bdellouridae, Tricladida: (A) *Pentacoelum*. Planariidae, Tricladida: (B) *Planaria*; (C) *Crenobia*; (D) *Polycelis*; (E) *Seidlia*; (F) *Plagnolia*; (G) *Phagocata*; (H) *Atrioplanari(A)* Dugesiidae, Tricladida: (I) *Schmidtea*; (J) *Girardia*; and (K) *Dugesia*.

Platyhelminthes: Tricladida: Planariidae: Genera

Body elongate, posterior and anterior end rounded, sometimes with pointed tentacles. Without adhesive disc. Coloration opaque, pigmented or whitish. With one pair eyes, or multiple eyes arranged in a row around the anterior margin or absent. Pharynx with one circular and one longitudinal muscular layer. Oviducts open combined into the atrium. Penis papillae elongated. Glandulomuscular organ or adenodactyls sometimes present. Shell glands open common oviduct.

1	Pigmentation pigmented (dark to yellow) 2
1′	Pigmentation milky-white 5
2(1)	Pointed tentacles absent; with two eyes 3
2′	Pointed tentacles present; with multiple eyes 4
3(2)	Anterior body end rounded; organ glandulomuscular or adenodactyl present (Fig. 5.4 B) ..... *Planaria*
3′	Anterior body end truncated and with prominent edges; organ glandulomuscular or adenodactyl absent (Fig. 5.4 C) ..... *Crenobia*
4(2)	Anterior body ends are different shapes; penis papillae elongated; organ glandulomuscular or adenodactyl sometimes present; spermiducal bulbs present; multiple eyes arranged in a marginal row at the anterior end (Fig. 5.4 D) ..... *Polycelis*
4′	Penis papillae conical short; organ glandulomuscular or adenodactyl absent; spermiducal bulbs absent; multiple eyes arranged in two symmetrical patches at the anterior end (Fig. 5.4 E) ..... *Seidlia*
5(1)	Two eyes present 6
5′	Eyes absent (Fig. 5.4 F) ..... *Plagnolia*
6(5)	Body with anterior end elongated and widen head; penis papillae conical short; organ glandulomuscular or adenodactyl absent (Fig. 5.4 G) ..... *Phagocata*
6′	Body with anterior end elongated and with a neck and head markedly narrower as the rest of the body; penis papillae elongated (Fig. 5.4 H) ..... *Atrioplanaria*

Platyhelminthes: Tricladida: Dugesiidae: Genera

Body shape elongated, anterior end triangular, posterior rounded. Coloration opaque, normally pigmented Without posterior adhesive disc. Eyes: one pair often surrounded by a circular depigmented area. Pharynx with one circular and one longitudinal muscular layer. Oviducts opens separate into the bursa canal. Spermiducal bulbs absent. Penis papillae elongated. Without glandulomuscular organ or adenodactyls (or rarely present). Shell glands open into the bursa stalk.

1	Pigmentation variable, from dark to beige, with spots or not; anterior body shape triangular; spermiducal bulbs present 2
1′	Pigmentation uniform brown; anterior body shape rounded; spermiducal bulbs absent (Fig. 5.4 I) ..... *Schmidtea*
2(1)	Auricles short and broad; anterior body tip bluntly pointed or rounded; shell glands open in the common oviduct (Fig. 5.4 J) ..... *Girardia*
2′	Auricles pointed; anterior body tip pointed; shell glands open into the bursa stalk (Fig. 5.4 K) ..... *Dugesia*

Platyhelminthes: Proseriata: Families

Body shape variable: oval, clavate, or elongate with rounded anterior end and posterior end pointed or truncated. Coloration with distinct pigmentations. Pharynx plicatus or variabilis, caudoventrally oriented. Brain with anterior and posterior lobes or trunks. Eyes present. Oral and genital pore separated. Ciliated pits sometimes present. Statocyst present. Refractile organs absent. Asexual reproduction absent. Testes follicular. Sclerotic male structures, in form of spines with different shapes and sizes present in some families. Orientation of male organ caudally. Female gonads ovary and yolk cells fully separated.

1	Body shape oval with pointed posterior end; brain ovoid without lobes; with paired eyes; ciliated pits present; male copulatory organ inerm, without spines; testes and vitellaria follicular lateral ..... **Otomesostomidae**
1′	Body shape elongated, filiform with rounded anterior end and posterior end pointed; brain ovoid; ciliated pits absent; male copulatory organ armed with spines; testes follicular median, vitellaria follicular laterally located (Fig. 5.5 D) ..... Coelogynoporidae, one genus: *Coelopgynopora*

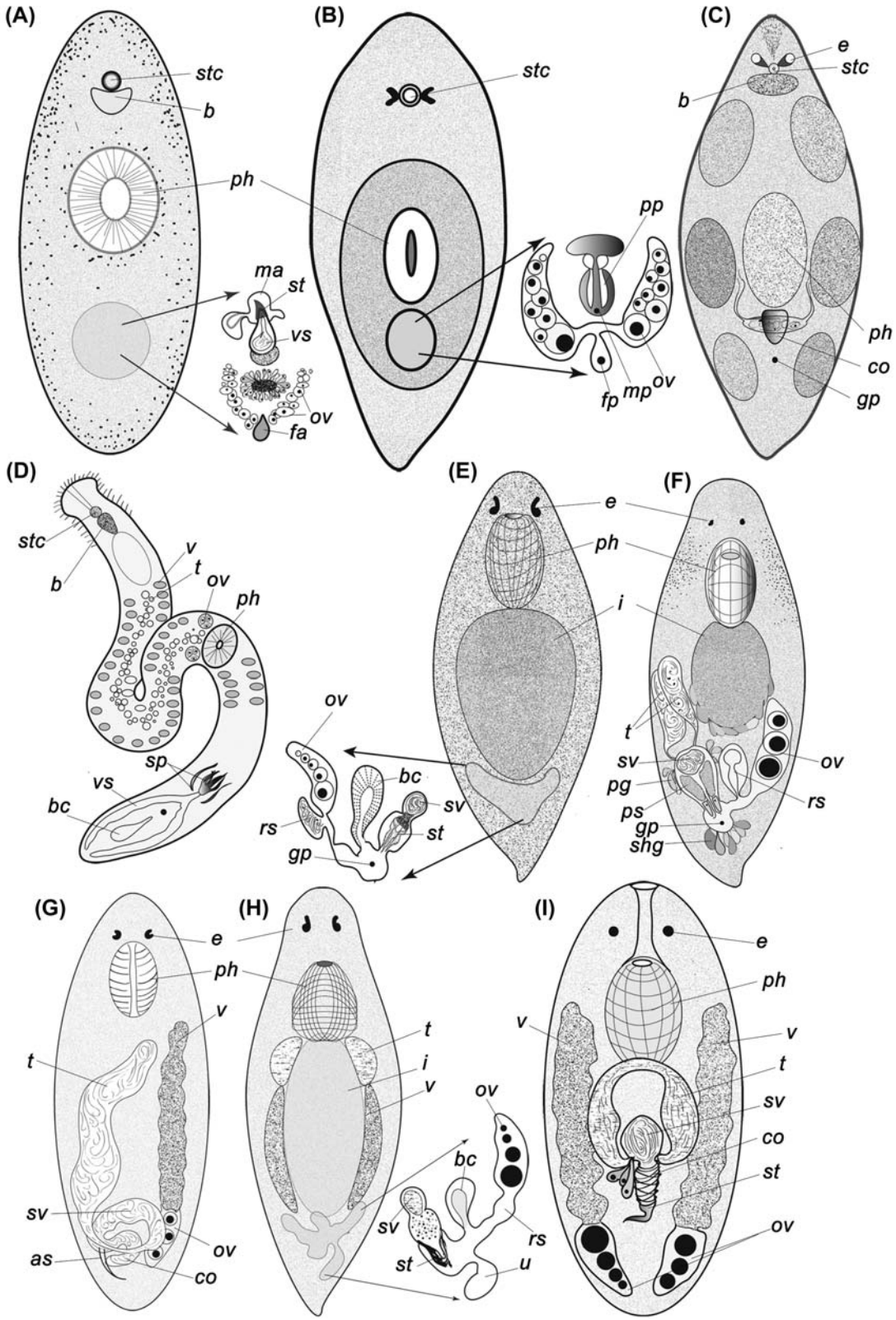


FIGURE 5.5 Otomesostomatidae, Proseriata: (A) *Baikalotomesostoma*; (B) *Otomesostom(A)* Proseriata: (C) *Japanoplan(A)* Coelogynoporidae, Proseriata: (D) *Coelogynopor(A)* Dalyelliidae, Rhabdocoela: (E) *Gieysztoria*; (F) *Sergi(A)* Provorticidae, Rhabdocoela: (G) *Eldenia*.; Dalyelliidae, Rhabdocoela: (H) *Microdalyelli(A)* Provorticidae, Rhabdocoela: and (I) *Baicalelli(A)*.

Platyhelminthes: Proseriata: Otomesostomidae: Genera

Body oval. Pigmentation yellow to reddish. Pharynx plicatus. Brain ovoid without lobes. Statocyst present. Refractile organs absent. Eyes present. Ciliated pits present. Oral and genital pore separated. Asexual reproduction absent. Testes paired, follicular chains situated laterally at the body. Male reproduction organ with sclerotized ductus ejaculatorius. Orientation of male organ caudally. Ovary or female gonads ovary and vitellaria fully separated. Vitellaria follicular and lateral.

1	Body pigmented; eyes present 2
1′	Body unpigmented; eyes absent; with two female genital pores (Fig. 5.5 A) ..... *Baikalomesostoma*
2(1)	Pigmentation grayish to yellowish-brownish reticulated; ciliated pits present; sclerotic male structures present (sclerotized ductus ejaculatorius); ovary and vitellaria fully separated (Fig. 5.5 B) ..... *Otomesostoma*
2′	Pigmentation distributed in symmetrical red-brownish patches; ciliated pits absent; sclerotic male structures absent (ductus ejaculatorius inerm); ovary and vitellaria not fully separated (Fig. 5.5 C) ..... *Japanoplana*

Platyhelminthes: Rhabdocoela: Suborders

Body oval or hastate with pointed posterior end. Pigmentation variable. Pharynx doliiformis (barrel-shaped) or rosulatus. Brain with anterior and posterior lobes. Eyes usually present. Oral and genital pores separated. Ciliated pits, statocyst or refractile organs absent. Asexual reproduction absent. Testes paired. Sclerotized male structures present with distinct shape and size, as cirrus or stylet, with spines or not. Orientation of male organ caudally. Ovary and yolk cells fully separated.

1	Pharynx rosulatus ventral oriented 2
1′	Pharynx doliiformis (cylindrical) frontal oriented, male copulatory organ with sclerotized structures like a stylet with variable shape and size at the posterior end ..... Dalyellida, one family: **Dalyelliidae**
2(1)	With conspicuous rhabdite rods, female and male gonopore common or close together, retractable anterior end. Testes paired, ovary usually single ..... Dalytyphoplanida, one family: **Typhloplanidae**
2′	With true proboscis with apex, muscular plates, splited or with hooks; usually testes and ovary paired; mainly marine ..... **Kalyptorhynchia**

Platyhelminthes: Rhabdocoela: Dalyellida: Dalyelliidae: Genera

Body fusiform, with rounded anterior end and pointed (tail) posterior end. Pharynx anterior, doliiformis or cylindrical, frontal oriented. Genital pore at the posterior end. Testes paired, compact. Male copulatory organ with complex sclerotized structure. Ovary smooth, unpaired. Vitellaria paired, smooth or papillary but not branched. Mainly with bursa copulatrix, without ductus spermaticus and with or without own receptaculum seminis. Uteri unpaired or in the female system included.

1	Body shape fusiform/elongate with rounded anterior end 2
1′	Body shape fusiform/elongate with truncated anterior end 8
2(1)	Pharynx cylindrical without longitudinal furrows, simple 3
2′	Pharynx cylindrical with a longitudinal furrow or furrows 6
3(2)	Testes located laterally at the posterior end 4
3′	Testes located laterally at the anterior end 5
4(3)	Ductus ejaculatorius armed with a stylet; stylet comprises a girdle with spines at the distal end; (Fig. 5.5 E) ..... *Gieysztoria*
4′	Ductus ejaculatorius inerm; without stylet or spines; (Fig. 5.5 F) ..... *Sergia*
5(3)	Coloration whitish translucent or opaque; vasa deferentia open together; stylet smooth curved tube with an accessory spine; smooth tubular vitellaria; (Fig. 5.5 G) ..... *Eldenia*
5′	Coloration brownish, reddish, yellowish; vasa deferentia open separated; stylet with proximal handle, central channel and distal spines; lobulated vitellaria; (Fig. 5.5 H) ..... *Microdalyellia*
6(2)	Coloration brownish, reddish, yellowish; testes elongate, clavate; vasa deferentia open together; stylet not infundibuliform 7
6′	Coloration whitish translucent or opaque; testes rounded; vasa deferentia open separately; stylet infundibuliform; (Fig. 5.5 I) ..... *Baicalellia*
7(6)	Testes located posteriolaterally; prostatic glands opening laterally, into the midproximal region of the male organ; ductus ejaculatorius armed with a stylet; stylet with anterior handles, without central channel and with spines; animal often green due to zoochlorellae; ..... (Fig. 5.6 A) ..... *Dalyellia*
7′	Testes located anteriolaterally; prostatic glands opening in the proximal region; ductus ejaculatorius inerm; without stylet, handles or spines; (Fig. 5.6 B) ..... *Pseudograffilla*

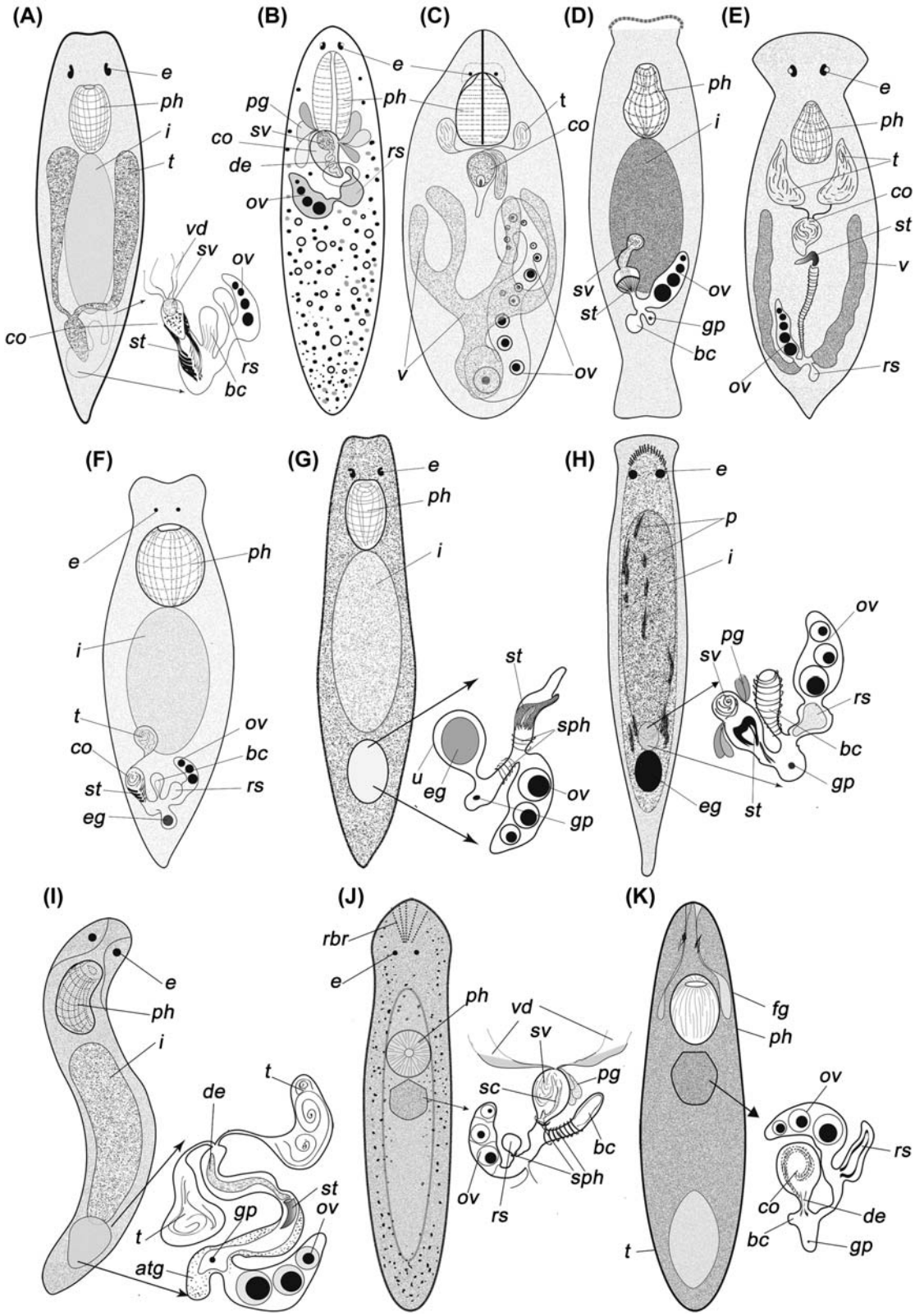


FIGURE 5.6 Dalyelliidae, Rhabdocoela: (A) *Dalyellia*; (B) Graffillidae, Rhabdocoela: *Pseudograffilla*; (C) *Bresslauilla*; Dalyelliidae, Rhabdocoela: (D) *Varsoviella*; (E) *Axiola*; (F), *Fulinskiella*; (G) *Castrella*; (H) *Vaillantiell(A)* Provorticidae, Rhabdocoela: (I) *Balgeti(A)* Typhloplanidae, Rhabdocoela: (J) *Strongylostoma*; and (K) *Lutheria.*

8(1)	Coloration whitish translucent or opaque	9
8′	Coloration brownish, reddish, yellowish	11
9(8)	Pharynx cylindrical without longitudinal furrows, simple; ductus ejaculatorius armed with a stylet; lobular or follicular vitellaria present	10
9′	Pharynx cylindrical with a longitudinal furrow or furrows; ductus ejaculatorius inerm; with smooth branched vitellaria; (Fig. 5.6 C)	*Bresslauilla*
10(9)	Testes rounded, posteriolateral; vasa deferentia openings separated; prostatic glands opening laterally into male organ midproximal region; stylet with girdle and spines; (Fig. 5.6 D)	*Varsoviella*
10′	Testes elongate, clavate, anteriolateral; vasa deferentia open together; prostatic glands opening into male organ proximal region; stylet curved, culullaform; (Fig. 5.6 E)	*Axiola*
11(8)	Stylet with handle and spines; ovary orientation caudal	12
11′	Stylet without handle and spines; ovary orientation anterior	13
12(11)	Prostatic glands open laterally, into the copulatory organ midproximal region; two stylets with one handle and spines; receptaculum seminis without stalk; (Fig. 5.6 F)	*Fulinskiella*
12′	Prostatic glands open proximally; one stylet with one handle and spines; receptaculum seminis with stalk; (Fig. 5.6 G)	*Castrella*
13(11)	Pharynx cylindrical without longitudinal furrows, simple; testes elongate, clavate; vasa deferentia open separated; stylet without girdle or handles, with spines of different shape and size and an accessory single spine; (Fig. 5.6 H)	*Vaillantiella*
13′	Pharynx cylindrical with longitudinal furrow or furrows; testes rounded; vasa deferentia open together; stylet infundibuliform; (Fig. 5.6 I)	*Balgetia*

Platyhelminthes: Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Subfamilies

Characteristic or few modified pharynx rosulatus; testes paired; ovary unpaired; male and female genital pores common; free living; inhabitants of fresh or brackish waters, sometimes in wet land biotopes.

1	Testes ventral to the vitellaria	2
1′	Testes dorsal to the vitellaria	5
2(1)	Eyes present (rarely absent); main excretory ducts open on excretory pouch (pharyngeal or atrial)	3
2′	Eyes absent; main excretory ducts open on body wall	4
3(2)	Ductus ejaculatorius sclerotized or with stylet; retractable anterior end absent; atrium copulatorium absent	**Typhloplaninae**
3′	Ductus ejaculatorius inerm, muscular; retractable anterior end present; atrium copulatorium present; spines present in bursa copulatrix or atrium copulatorium	**Rhynchomesostominae**
4(2)	Pharynx ventrally oriented and centrally located; ductus ejaculatorius inerm, muscular; main excretory opening separate at the body wall	**Protoplanellinae**
4′	Pharynx caudally oriented and posteriorly located; ductus ejaculatorius with spines, cirrus-like; main excretory opening common between oral and genital pore	Opistominae, one genus: *Opistomum*
5(1)	Ductus ejaculatorius sclerotized or with spines	6
5′	Ductus ejaculatorius inerm, muscular	7
6(5)	Pharynx anteriorly oriented and located; vitellaria plumiform or digitiform; testes compact elongate organs behind the pharynx; main excretory opening location on body wall	Phaenocorinae, one genus: *Phaenocora*
6′	Pharynx ventrally oriented and centrally located; vitellaria lightly lobulated or smooth tubes; testes compact (clavate or elongate) in front and/or next to the pharynx; main excretory opening location on pharyngeal excretory pouch	**Mesostominae**
7(5)	Eyes usually present; bursa copulatrix, when present, stalked; without ascus	Olisthanellinae, one genus: *Olisthanella*
7′	Eyes absent; bursa copulatrix, when present, with a broad stalk; with ascus	**Ascophorinae**

Platyhelminthes: Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Typhloplaninae: Genera

Body anteriorly and posteriorly rounded. Cross section rounded. Pigmentation whitish or yellowish, sometimes opaque. Without retractable anterior end. Eyes sometimes present. Rhabdite rods present. Pharynx rosulatus ventrally oriented. Main excretory trunk with separate opening. Oral and genital pore separated. Testes clavate or elongate, ventral to the vitellaria and in front and/or next to the pharynx. Reproductive complex in central or posterior body. Copulatory organ pyriform and caudally oriented. Ductus ejaculatorius inerm, sclerotic, or armed. Bursa copulatrix when present a sac-like organ with a broad stalk. Vitellaria smooth or lightly lobulated tubes. Receptaculum seminis present. Uteri: unpaired. Atrium genitale communis simple or differentiated in superior and inferior atrium.

1	Pharynx positioned anteriorly	2
1′	Pharynx positioned centrally	5
2(1)	Eyes present	3
2′	Eyes absent	4
3(2)	Ductus ejaculatorius armed with a cirrus; opening to prostatic glands proximally; vasa deferentia tubular with dilatations (external of false vesicula seminalis); (Fig. 5.6 J)	*Strongylostoma*
3′	Ductus ejaculatorius unarmed not sclerotic; opening of prostatic glands laterally; vasa deferentia tubular without dilatations; (Fig. 5.6 K)	*Lutheria*
4(2)	Receptaculum seminis present with stalk, ductus ejaculatorius sclerotized; (Fig. 5.7 A)	*Typhloplana*
4′	Receptaculum seminis present without stalk (enclosed in the female canal), ductus ejaculatorius sclerotized; (Fig. 5.7 B)	*Kambanella*
5(1)	Ductus ejaculatorius armed	6
5′	Ductus ejaculatorius unarmed	8
6(5)	With a stylet; atrium genitale communis simple	7
6′	With cirrus; atrium genitale communis differentiated in superior and inferior; (Fig. 5.7 C)	*Vranjella*
7(6)	Stylet with girdle and spines; receptaculum seminis present with stalk; (Fig. 5.7 D)	*Limnoruanis*
7′	Stylet straight (aciculate or turriform); receptaculum seminis present without stalk (enclosed in the female canal); (Fig. 5.7 E)	*Stygoplanella*
8(5)	Without eyes; vasa deferentia tubular without dilatations; prostatic glands open laterally into the male organ; bursa copulatrix present; (Fig. 5.7 F)	*Typhloplanella*
8′	With eyes; vasa deferentia tubular with dilatations (external to false vesicula seminalis); prostatic glands opening proximally into the male organ; bursa copulatrix absent (Fig. 5.7 G)	*Jovanella*

Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Rhynchomesostominae: Genera

Body fusiform with anterior end retractable and posteriorly bluntly pointed. Cross section rounded. Eyes sometimes present. Adenal and dermal rhabdites, as well as rhabdite rods present. Pharynx rosulatus central (at the middle of body) and ventrally oriented. Main excretory opening separate on excretory pouch (pharyngeal or atrial). Oral and genital pores close together or common. Testes clavate-elongate, ventral to the vitellaria and in front and/or next to the pharynx. Vasa deferentia tubular without dilatations. Reproductive complex central or posterior. Copulatory organ pyriform, caudally oriented. Penis papilla conical. Ductus ejaculatorius inerm, muscular. Bursa copulatrix when present sac-like with a broad stalk. Atrium copulatorium present in some genera. Spines present in the bursa copulatrix or the atrium copulatorium. Vitellaria smooth or lightly lobulate tubes. Receptaculum seminis present. Ducto genito-intestinalis absent. Uteri paired. Atrium genitale communis differentiated in superior and inferior.

1	Retractable anterior end absent; male copulatory organ caudally oriented	2
1′	Retractable anterior end present; male copulatory organ frontally oriented	5
2(1)	Eyes present; atrium copulatorium without blind sacs	3
2′	Eyes absent; atrium copulatorium with blind sacs	4
3(2)	Copulatory organ pyriform; testes compact elongate organs behind the pharynx; atrium copulatorium without spines; (Fig. 5.7 H)	*Papiella*
3′	Copulatory organ oval; testes compact clavate organs in front and next to the pharynx; atrium copulatorium present with spines; (Fig. 5.7 I)	*Mesocastrada*
4(2)	Spines of atrium copulatorium or of the blind sacs present, but not in plates; receptaculum seminis present without stalk (rounded); (Fig. 5.8 A)	*Castrada*
4′	Spines of the atrium copulatorium or the blind sacs present in plates; receptaculum seminis with stalk; (Fig. 5.8 B)	*Castradella*
5(1)	Pharynx anterior (before the body center), frontally oriented; two pairs of eyes; reproductive complex located behind the pharynx in the first body half; copulatory organ oval, vasa deferentia openings common; (Fig. 5.8 C)	*Tetracelis*
5′	Pharynx central (at the middle of body) ventrally oriented; one pair of eyes; reproductive complex located behind the pharynx in the last body half; copulatory organ pyriform, vasa deferentia openings separated; (Fig. 5.8 D)	*Rhynchomesostoma*

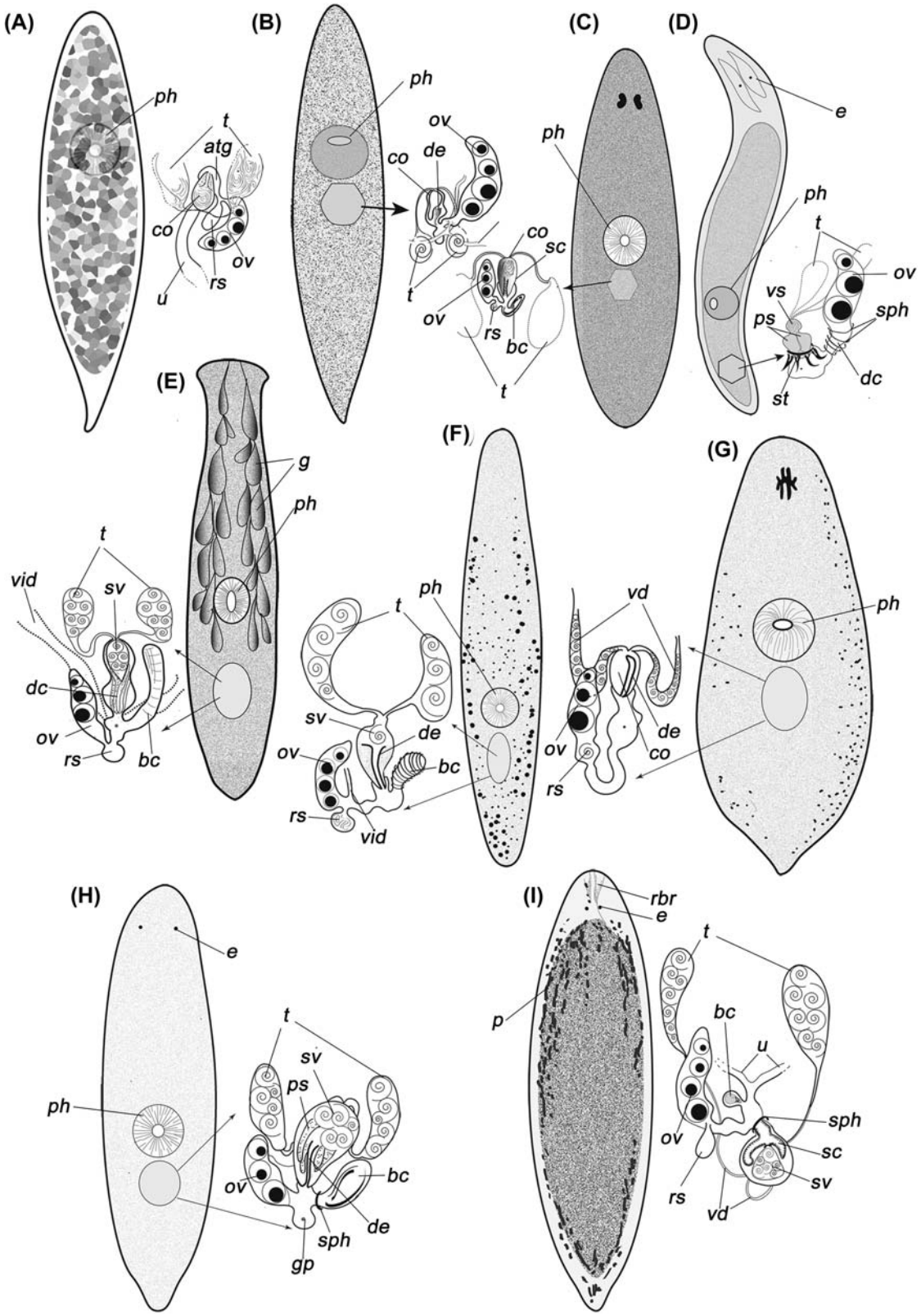


FIGURE 5.7 Typhloplanidae, Rhabdocoela: (A) *Typhloplana*; (B) *Kambanella*; (C) *Vranjella*; (D) *Limnoruanis*; (E) *Stygoplanella*; (F) *Typhloplanella*; (G) *Jovanell(A)* (H) *Papiella*; and (I) *Mesocastrada*.

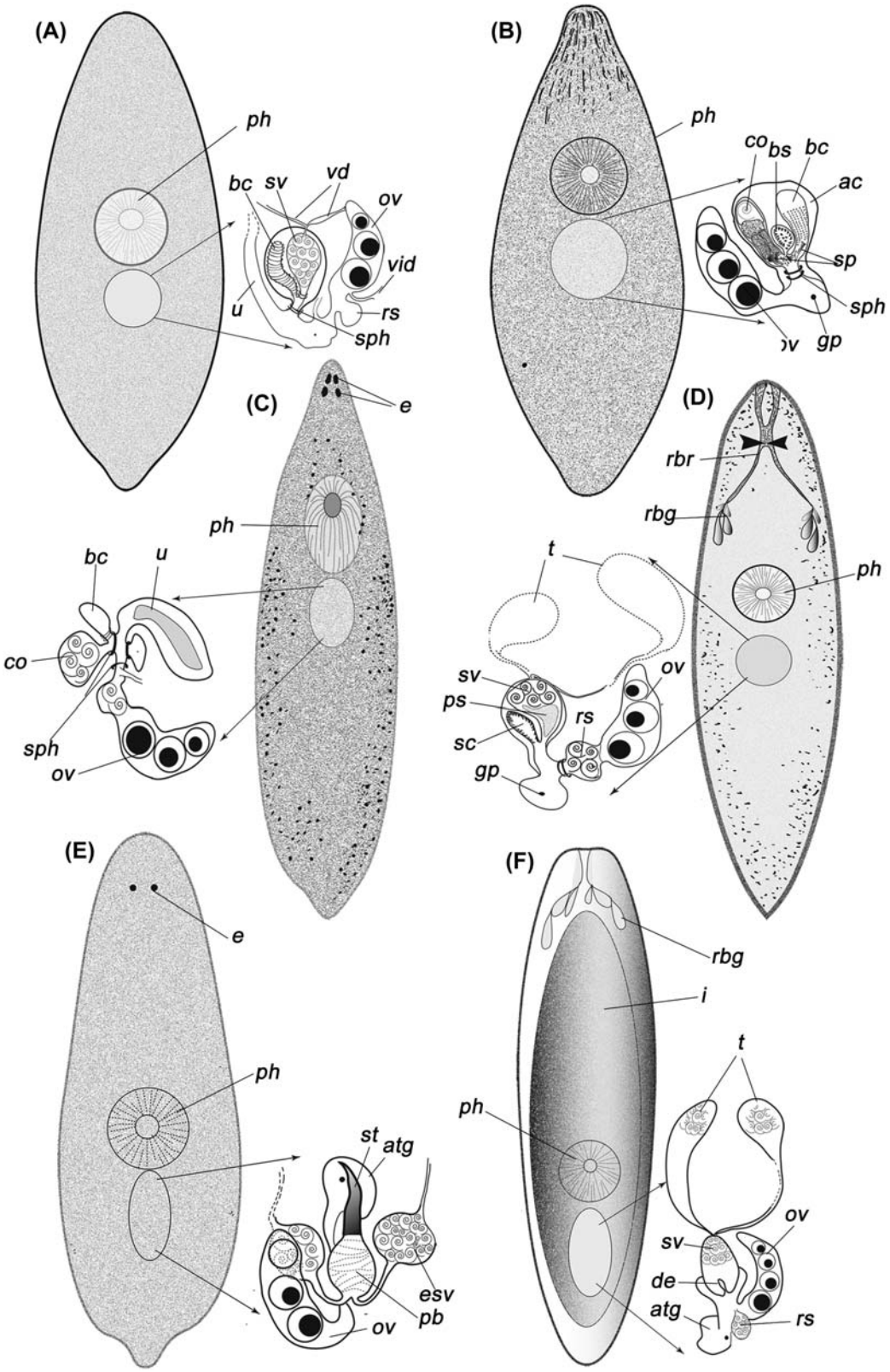


FIGURE 5.8 Typhloplanidae, Rhabdocoela: (A) *Castrada*; (B) *Castradella*; (C) *Tetracelis*; (D) *Rhynchomesostoma*; (E) *Proamphibolella*; and (F) *Olisthanellinella*;

Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Protoplanellinae: Genera

Body fusiform with tapered or rounded anterior end and bluntly pointed posterior end. Cross section rounded. Retractable anterior end absent. Eyes usually absent. Adenal and dermal rhabdites absent, but with rhabdite rods. Pharynx rosulatus central (at the middle of body) orientation ventral. Main excretory opening separate on body wall. Oral and genital pores separated. Testes clavate or elongate, in front or next to the pharynx and ventral to the vitellaria. Vasa deferentia tubular without dilatations. Reproductive complex in the posterior body half. Copulatory organ pyriform, caudally oriented. Penis papilla short. Ductus ejaculatorius inerm and muscular. Bursa copulatrix when present sac-like with a broad stalk. Without atrium copulatorium. Without spines. Vitellaria smooth or lightly lobulated tubes. Receptaculum seminis and ducto genito-intestinalis absent. Uteri unpaired. Atrium genitale communis simple.

1	Testes clavate anteriorly, and next to the pharynx	2
1′	Testes clavate posteriorly behind the pharynx	9
2(1)	Oral and genital pores separated, but in the same body third	3
2′	Oral and genital pores widely separated, in different body thirds	6
3(2)	Vasa deferentia tubular with dilatations	4
3′	Vasa deferentia tubular without dilatations	5
4(3)	Copulatory organ pyriform; ductus ejaculatorius sclerotized, tubular; bursa copulatrix absent; eyes present reniform or rounded; (Fig. 5.8 E)	*Proamphibolella*
4′	Copulatory organ oval; ductus ejaculatorius no sclerotized, cirrus-like; bursa copulatrix present; eyes absent (Fig. 5.8 F)	*Olisthanellinella*
5(3)	Ductus ejaculatorius sclerotized; bursa copulatrix without spines; (Fig. 5.9 A)	*Krumbachia*
5′	Ductus ejaculatorius not sclerotized; bursa copulatrix with spines; (Fig. 5.9 B)	*Chorizogynopora*
6(2)	Copulatory organ pyriform	7
6′	Copulatory organ oval	8
7(6)	Bursa copulatrix with spines; ductus ejaculatorius tubular, without spines; vitellaria lobulated; (Fig. 5.9 C)	*Hoplopera*
7′	Bursa copulatrix without spines; ductus ejaculatorius cirriform with spines; vitellaria smooth tubes; (Fig. 5.9 D)	*Rhomboplanilla*
8(6)	Ductus ejaculatorius tubular with spines; vitellaria smooth tubes; vasa deferentia openings common; (Fig. 5.9 E)	*Olisthanelliola*
8′	Ductus ejaculatorius tubular without spines; vitellaria lobulated; vasa deferentia openings separated; (Fig. 5.9 F)	*Perandropora*
9(1)	Pharynx in middle of the body	10
9′	Pharynx anterior	13
10(9)	Ductus ejaculatorius sclerotized or with spines	11
10′	Ductus ejaculatorius not sclerotized, inerm	12
11(10)	Pharynx orientation frontal; oral and genital pore separated, but in the same body third; vasa deferentia openings separated; vitellaria smooth tubes; (Fig. 5.9 G)	*Adenocerca*
11′	Pharynx orientation ventral; oral and genital pores well separated, in different body thirds; vasa deferentia openings common; vitellaria lobulated; (Fig. 5.10 A)	*Amphibolella*
12(10)	Copulatory organ pyriform; bursa copulatrix absent; main excretory ducts opening separate on body wall; receptaculum seminis included in the ductus communis; (Fig. 5.10 B)	*Pseudobockia*
12′	Copulatory organ oval; bursa copulatrix present; main excretory duct openings separate in the pharynx pouch; receptaculum seminis absent; (Fig. 5.10 C)	*Protoplanella*
13(9)	Oral and genital pores well separated, in different body thirds; rhabdite rods present; pigmentation whitish-yellowish; bursa copulatrix present	14
13′	Oral and genital pores separated, but in the same body third; rhabdite rods absent; dark pigmentation at the dorsal region; bursa copulatrix absent; (Fig. 5.10 D)	*Bockia*
14(13)	Vasa deferentia openings separated; copulatory organ oval; ductus ejaculatorius cirriform with spines; (Fig. 5.10 E)	*Acrochordonoposthia*
14′	Vasa deferentia openings common; copulatory organ pyriform; ductus ejaculatorius tubular without spines; (Fig. 5.10 F)	*Propharyngiellona*

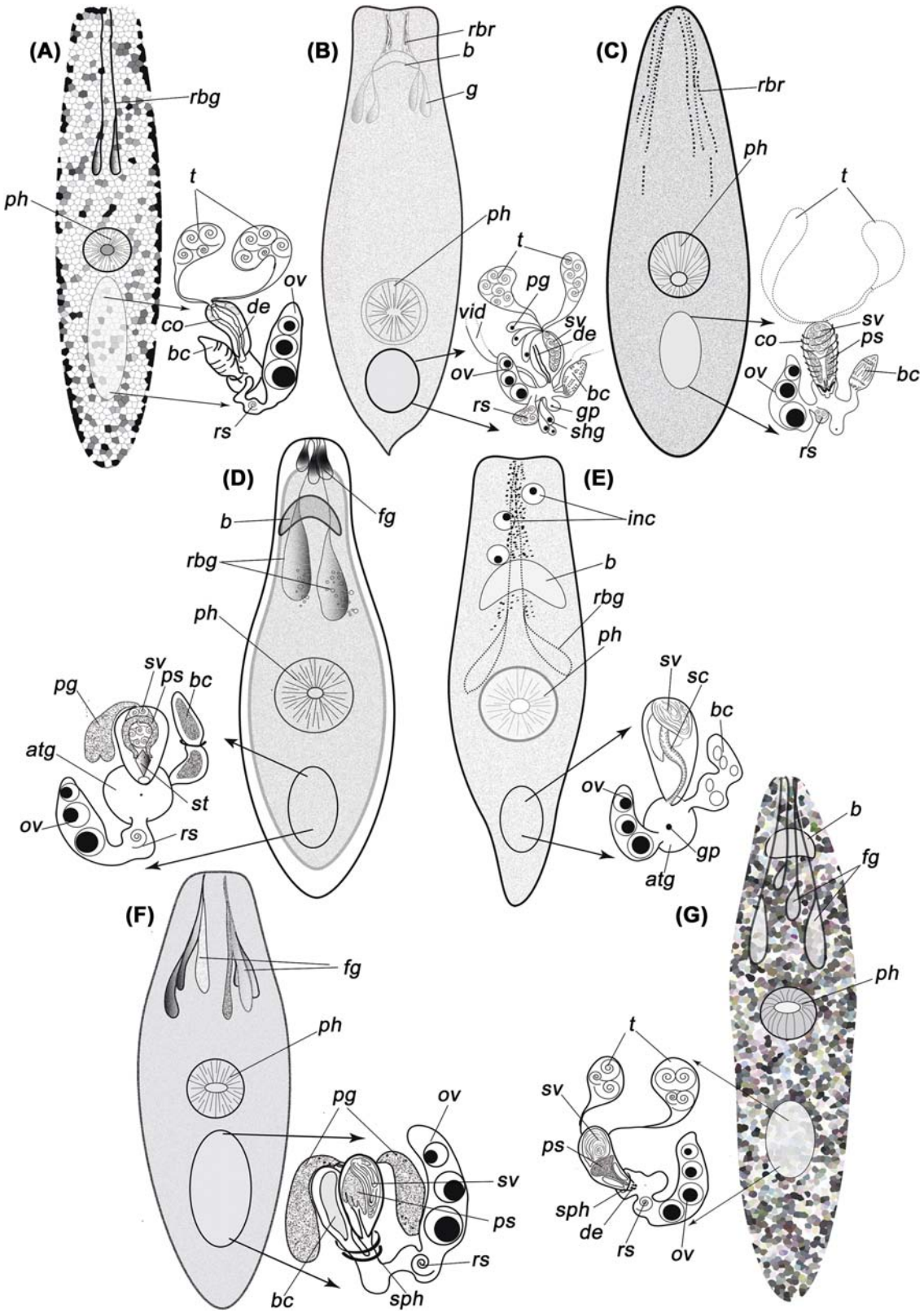


FIGURE 5.9 Typhloplanidae, Rhabdocoela: (A) *Krumbachia*; (B) *Chorizogynopora*; (C) *Hoplopera*; (D) *Rhomboplanilla*; (E) *Olisthanelliola*; (F) *Perandropora*; and (G) *Adenocerca*.

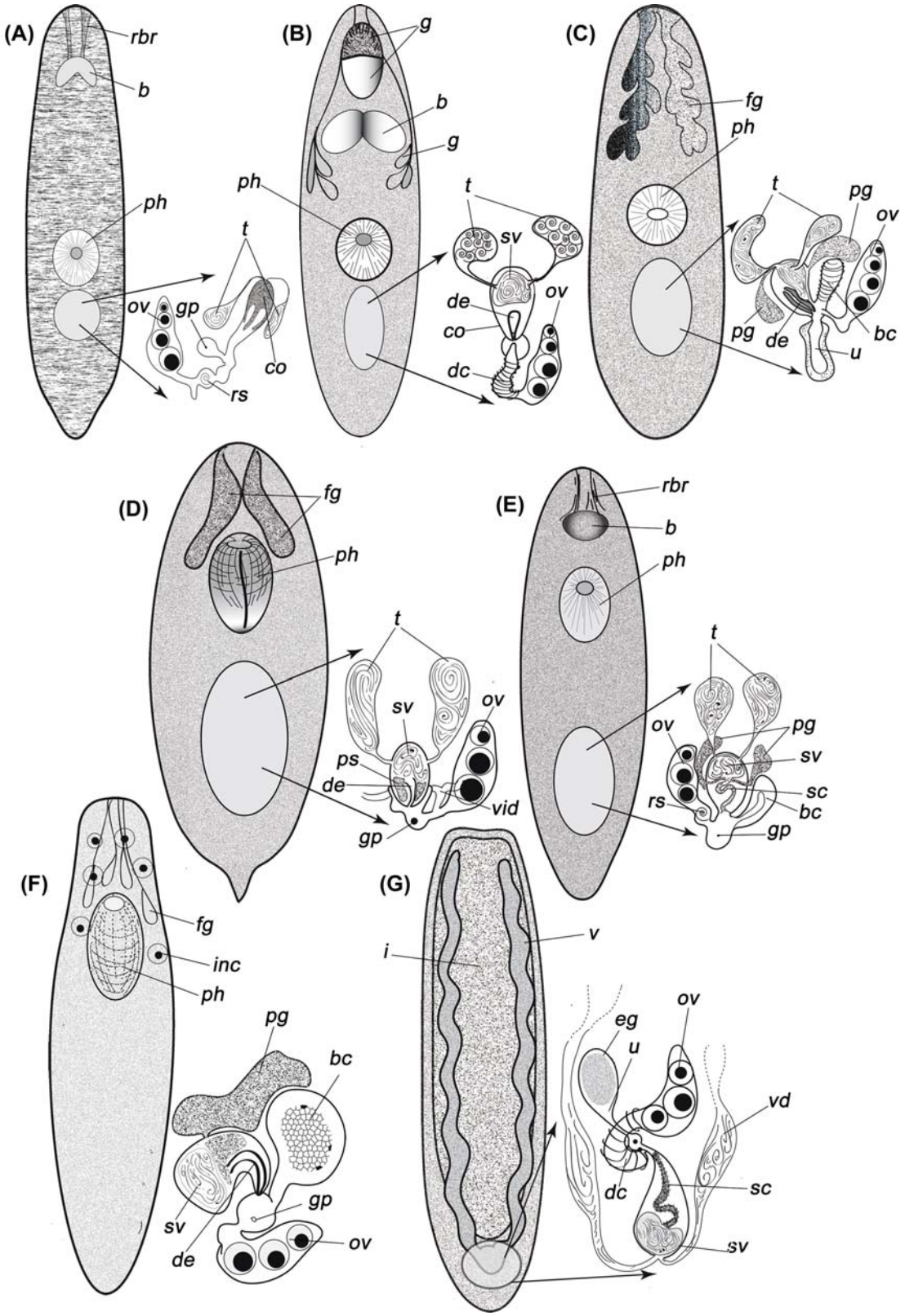


FIGURE 5.10 Typhloplanidae, Rhabdocoela: (A) *Amphibolella*; (B) *Pseudobockia*; (C) *Protoplanella*; (D) *Bockia*; (E) *Acrochordonoposthia*; (F) *Propharyngiellona*; and (G) *Opistomum*.

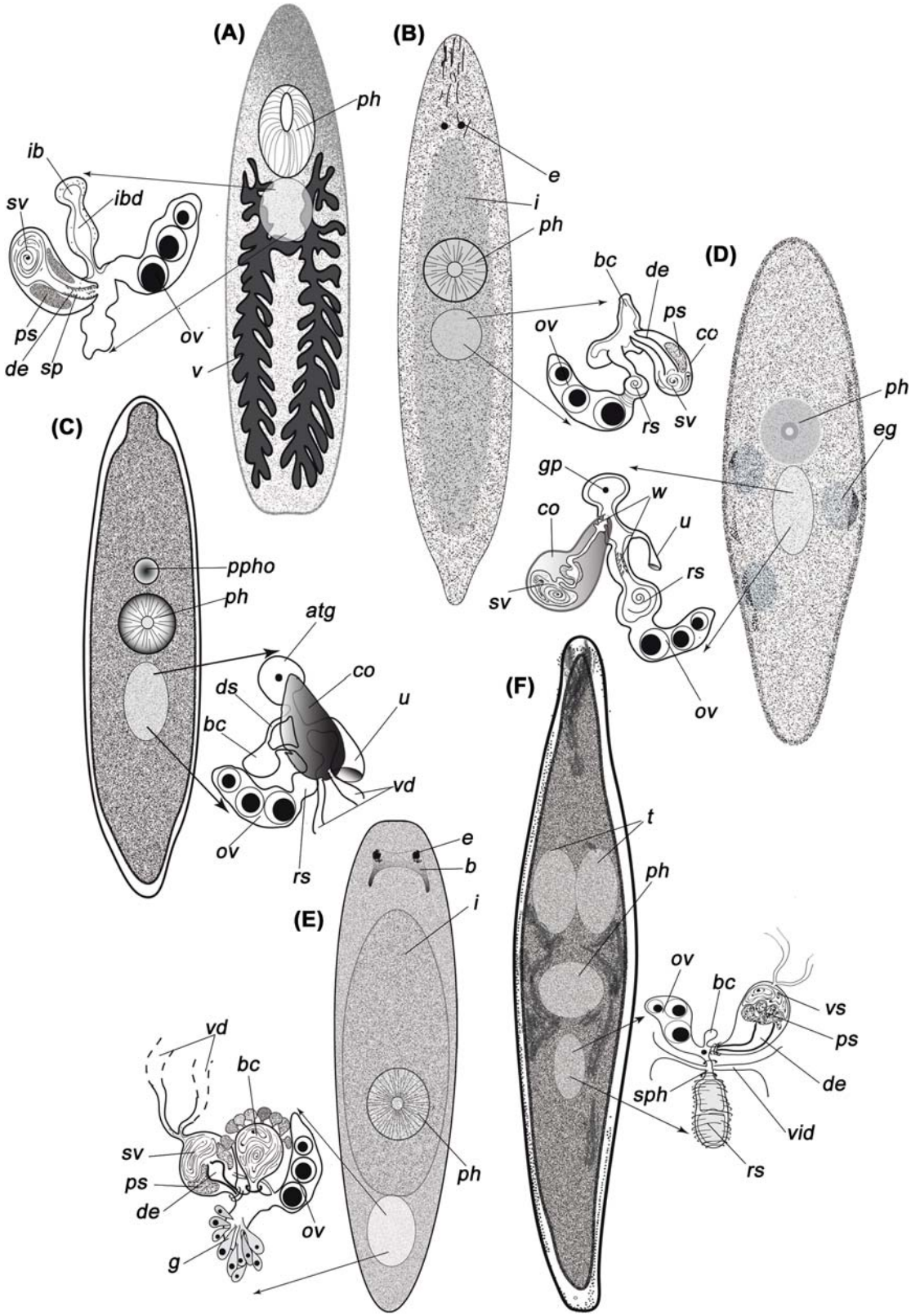


FIGURE 5.11 Typhloplanidae, Rhabdocoela: (A) *Phaenocora*; (B) *Mesostoma*; (C) *Bothromesostoma*; (D) *Marcomesostoma*; (E) *Olisthanella*; and (F) *Ascophora*.

Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Mesostominae: Genera

Body fusiform with tapered or rounded anterior end and the posterior end bluntly pointed. Cross section oval and flattened. Anterior end sometimes retractable or very flexible. Eyes present. Adenal and dermal rhabdites present, as well as rhabdite rods. Pharynx rosulatus central (at middle of body) ventrally oriented. Main excretory opening separated, on excretory pouch (pharyngeal or atrial). Oral and genital pores close together or common. Testes clavate or elongate dorsal to vitellaria and in front of and/or next to the pharynx. Vasa deferentia tubular without dilatations. Reproductive complex central or posterior. Copulatory organ pyriform, caudally oriented. Penis papilla conical. Ductus ejaculatorius mainly sclerotized, and sometimes with spines. Bursa copulatrix when present, sac-like with a stalk. Vitellaria: smooth or light lobulated tubes. Receptaculum seminis present. Uteri paired. Atrium genitale communis simple.

1 Body shape fusiform with rounded anterior end and posterior end pointed; dorsally convex and ventrally flattened; eyes rounded without anastomosis; pharynx positioned in the second body third (behind the body middle) 2

1′ Body shape fusiform with anterior and posterior end pointed or with a posterior tail; cross section rounded or flattened; eyes sometimes anastomosed; pharynx in anterior body third; (Fig. 5.11 B) ..... *Mesostoma*

2(1) Anterior end not retractable; highly pigmented (dark or chocolate brown with a pale border); prepharyngeal pit present; copulatory organ oriented ventrally, ductus ejaculatorius not sclerotized; (Fig. 5.11 C) ..... *Bothromesostoma*

2′ Anterior end retractable; lightly pigmented (beige); prepharyngeal pit absent; copulatory organ oriented posteriorly; ductus ejaculatorius cirriform; (Fig. 5.11 D) ..... *Marcomesostoma*

Rhabdocoela: Dalytyphoplanida: Typhloplanidae: Ascophorinae: Genera

Body anterior and posterior ends rounded. Cross section rounded. Without retractable anterior end. Eyes absent. Adenal and dermal rhabdites absent. Rhabdite rods present. Pharynx rosulatus central, at the body middle and ventrally oriented. Main excretory trunks open separately on body wall. Oral and genital pores separated. Testes clavate or elongate, dorsal to the vitellaria and in front of and/or next to the pharynx. Vasa deferentia tubular with dilatations (sperm vesicles or bulbs). Reproductive complex central or posterior. Copulatory organ oval, posteriorly oriented. Penis papilla short. Ductus ejaculatorius inerm, muscular. Bursa copulatrix when present, sac-like with a broad stalk. Atrium copulatorium absent. Vitellaria: smooth or light lobulated tubes. Receptaculum seminis present. Uteri unpaired. Ascus present. Atrium genitale communis simple.

1 Reproductive organs near body center; vitellaria behind the pharynx; testes in front of vitellaria and pharynx; (Fig. 5.11 F) ..... *Ascophora*

1′ Reproduction organs in posterior body third, vitellaria next to and in front of the pharynx; testes dorsal to the vitellaria; (Fig. 5.12 A) ..... *Dochmiotrema*

Platyhelminthes: Rhabdocoela: Kalyptorhynchia: Families

Rhabdocoela with an anterior proboscis, inerm or with hooks, muscular plates or ampule. Rosulate pharynx. Paired testes; with single or paired ovary and with or without sclerotic structures at the end of the male copulatory organ (ductus ejaculatorius).

1 Ovaries paired 2

1′ Ovary unpaired 4

2(1) Proboscis not split, without muscular plates; eyes reniform or rounded without anastomosis; male copulatory organ without teeth 3

2′ Proboscis split, with muscular plates; eyes absent; male copulatory organ with teeth; (Fig. 5.12 B) ..... Placorhynchidae, one species: *Placorhynchus dimorphis* Karling, 1947

3(2) Proboscis with apex; pharynx anterior; proboscis without ampullae; male copulatory organ without cirrus, with teeth or stylet ..... **Koinocystidae**

3′ Proboscis without apex; pharynx central or posterior; proboscis with ampullae; cirrus present; (Fig. 5.13 A) ..... Cicerinidae, one species: *Ethmorhynchus youngi* Kolasa, 1977

4(1) Proboscis not split; eyes present reniform or rounded, without anastomosis; male copulatory organ with stylet 5

4′ Proboscis split with distal hooks and lateral glands; eyes absent; male copulatory organ with cirrus ..... **Karkinorhynchidae**

5(4) Proboscis with apex present; pharynx anterior; testes clavate, paired; granular secretion packing in a true prostatic vesicle, separated from the vesicula seminalis ..... **Polycystidae**

5′ Proboscis with two hooks; pharynx central or posterior; testes unpaired, elongated; granular secretion free, but packet in bunch; (Fig. 5.13 H) ..... Gnathorhynchidae, one species: *Uncinorhynchus karlingi* Kolasa, 1977

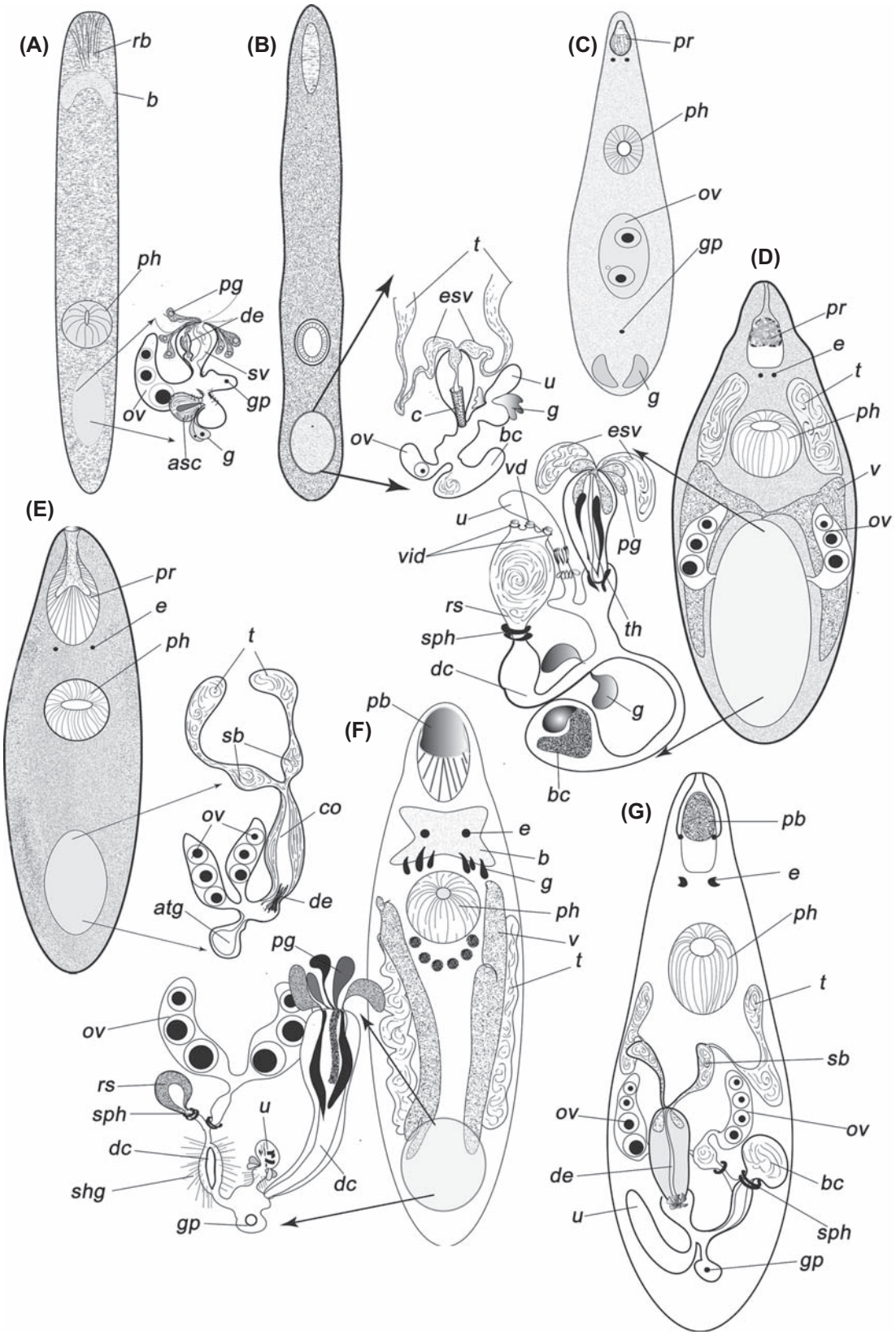


FIGURE 5.12 Typhloplanidae, Rhabdocoela: (A) *Dochmiotrem(A)* Placorhynchidae, Rhabdocoela: (B) *Placorhynchus*; Koinocystidae, Rhabdocoela: (C) *Sekerana*; (D) *Brunetia*; (E) *Koinocystis*; (F) *Pontarallia*; and (G) *Utelga*.

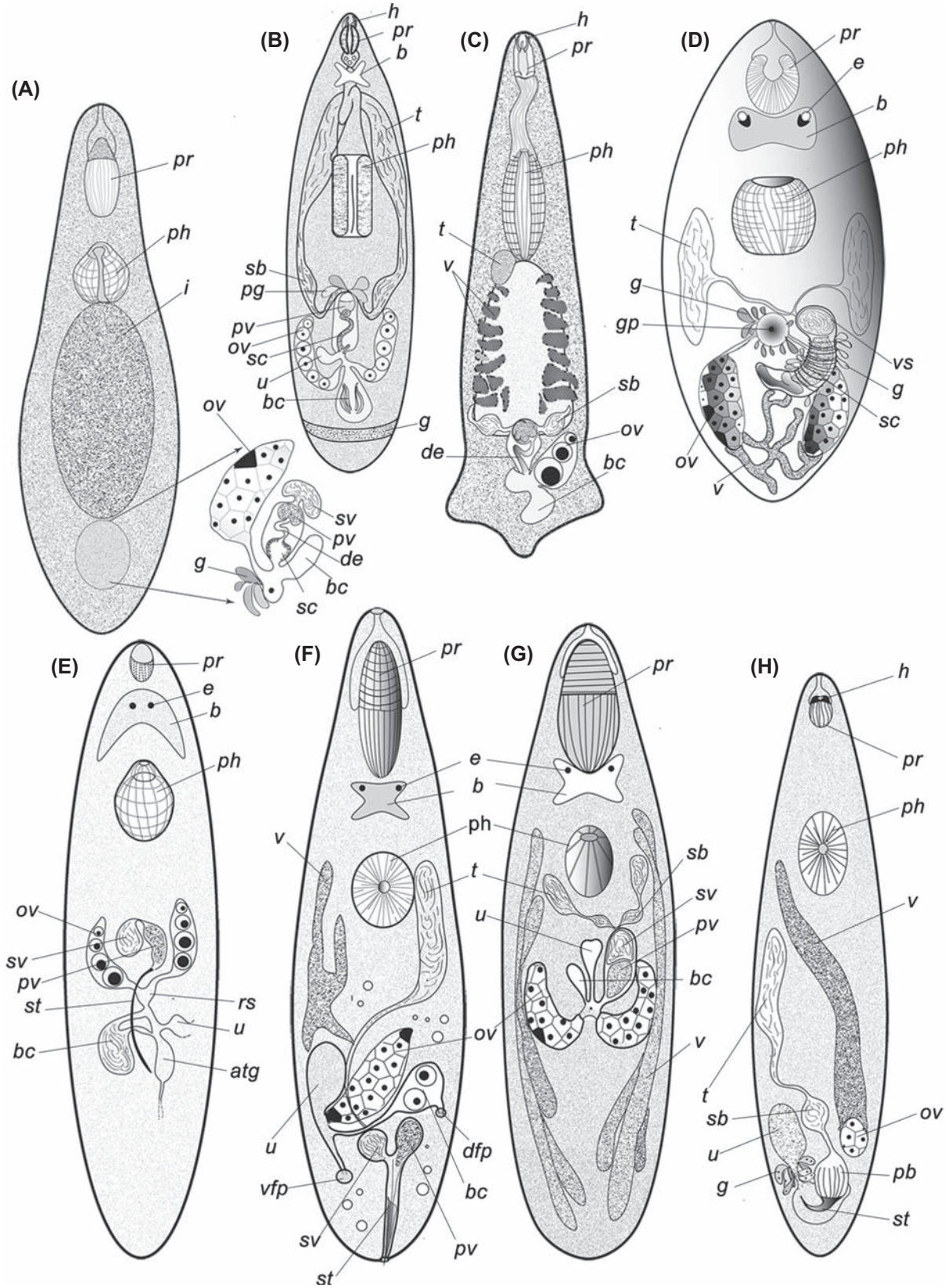


FIGURE 5.13 Cicerinidae, Rhabdocoela: (A) *Ethmorhynchus*. Karkinorhynchidae, Rhabdocoela: (B) *Baltoplana*; (C) *Cheliplan(A)* Polycistidae, Rhabdocoela: (D) *Acrorhynchides*; (E) *Djeziraia*; (F) *Gyratrix*; (G) *Opisthocystis*. Gnathorhynchidae, Rhabdocoela: and (H) *Uncinorhynchus*.

Platyhelminthes: Rhabdocoela: Kalyptorhynchia: Koinocystidae: Genera

Body elongate, anterior and posterior ends rounded. Proboscis not split, without ampullae, hooks, or muscular plates, but with apex. Pharynx anterior. Eyes present, reniform or rounded without anastomosis. Testes clavate, paired. Granular secretion free, but packed in bunch. Male copulatory organ with teeth or stylet, sometimes unarmed. Vitellaria smooth and paired. Ovary paired.

1	Testes anterior, compact, clavate 2
1′	Testes unpaired, ovoid; male reproductive system very reduced, inconspicuous; female system well-developed vitellaria U-shaped, ovary oval and unpaired; (Fig. 5.12 C) ..... *Sekerana*
2(1)	Testes in front of, or next to the pharynx; cirrus absent 3
2′	Testes just behind pharynx; cirrus present 4
3(2)	Ductus ejaculatorius with stylet and two loose teeth; vitellaria paired smooth tubes; (Fig. 5.12 D) ..... *Brunetia*
3′	Ductus ejaculatorius with a toothed stylet (forked); vitellaria paired and lobular; (Fig. 5.12 E) ..... *Koinocystis*
4(2)	With conspicuous distal teeth and spiny cirrus; vitellaria lobular; vasa deferentia tubular with dilatations (external seminal vesicle); ovary paired; (Fig. 5.12 F) ..... *Pontarallia*
4′	Without conspicuous distal teeth; with spiny cirrus; vitellaria smooth tubes; vasa deferentia tubular without dilatations; ovary unpaired; (Fig. 5.12 G) ..... *Utelga*

Platyhelminthes: Rhabdocoela: Kalyptorhynchia: Karkinorhynchidae: Genera

Body elongate, anterior and posterior ends rounded. Proboscis split, without ampullae or muscular plates or apex, but with hooks. Pharynx central or posterior. Eyes absent. Testes unpaired, elongate. Granular secretion with a true prostatic vesicle, separated from the seminal vesicle. Stylet absent. Male copulatory organ without stylet, but with teeth or spiny cirrus. Vitellaria paired. Ovary unpaired.

1	Testes compact, elongated organs, horseshoe shaped; vitellaria smooth tubes; vaginal pore absent; ovary paired, male copulatory organ armed with a spiny cirrus ending in a widening; (Fig. 5.13 B) ..... *Baltoplana*
1′	Testes unpaired; vitellaria lobular; vaginal pore present; ovary unpaired; male copulatory organ mainly with a spiny cirrus; (Fig. 5.13 C) ..... *Cheliplana*

Platyhelminthes: Rhabdocoela: Kalyptorhynchia: Polycystidae: Genera

Body with anterior end slight pointed, posterior end rounded. Proboscis not split, without ampullae, hooks, or muscular plates but with apex. Pharynx anterior. Eyes present reniform or rounded without anastomosis. Testes clavate, paired. Granular secretion packing in a true vesicula granulorum, separated from the vesicula seminalis. Male copulatory organ armed with stylet. Vitellaria paired. Ovary unpaired or paired.

1	Pharynx anteriorly oriented and at the anterior end; testes clavate, just behind the pharynx 2
1′	Pharynx ventrally oriented, near body middle; testes elongate or clavate 3
2(1)	Copulatory organ with teeth and without stylet; (Fig. 5.13 D) ..... *Acrorhynchides*
2′	Copulatory organ without teeth and with straight stylet; (Fig. 5.13 E) ..... *Djeziraia*
3(1)	Pigmentation translucent yellow to brown or green; vasa deferentia tubular without dilatations; male copulatory organ with straight stylet, ovary unpaired; (Fig. 5.13 F) ..... *Gyratrix*
3′	Pigmentation translucent gray-yellow; vasa deferentia tubular with dilatations (external of false seminal vesicle); male copulatory organ muscular, inerm, without sclerotic structures; ovary paired; (Fig. 5.13 G) ..... *Opisthocystis*

Platyhelminthes: Macrostomida: Families

Pigmentation variable, whitish to brown or reddish. Pharynx simplex. Brain with anterior and posterior lobes. Eyes present. Oral and genital pores separated. Ciliated pits present. Statocyst or refractile organs absent. Asexual reproduction present. Testes paired. Sclerotized male structures, like stylets, present. Male organ posterior. Ovary and yolk cells fully separated. Freshwater or marine.

1	Body shape elongate or clavate with posterior end truncated; eyes present; brain with anterior and posterior lobes; preoral blind sac of the gut absent; ciliated sensory pits absent ..... **Macrostomidae**
1′	Body shape elongate with transverse septa (zooids); brain ovoid without lobes; without eyes; preoral blind sac of the gut present; ciliated sensory pits present ..... **Microstomidae**

Platyhelminthes: Macrostomida: Macrostomidae: Genera

With sexual but not asexual reproduction. Male stylet oriented posteriorly. Ovary paired.

1 Body posterior end truncated, with an adhesive plate; second female pore bursa absent 2

1′ Body posterior end spatulate with adhesive glands; second female pore bursa present, stylet infundibuliform, thickened distally; ..... (Fig. 5.14 A) ..... *Promacrostomum*

2(1) Male stylet infundibuliform or elongate without accessory structures or thickening; coloration pigment less to brownish or reddish; (Fig. 5.14 B) ..... *Macrostomum*

2′ Male stylet infundibuliform, proximal region campanuliform; coloration translucent, sometimes brownish to gut content; (Fig. 5.14 C) ..... *Omalostomum*

Platyhelminthes: Macrostomida: Microstomidae: Genera

With both sexual and asexual reproduction. Male stylet oriented anteriorly. Ovary unpaired.

1 Body with a tail; without eyes; ciliated sensory pits present dorsal; intestine level muscle ring present; (Fig. 5.14 D) ..... *Myozonella*

1′ Body with transversal septa (zooids), lacking a conspicuous tail; paired pigment patches reddish to brownish; ciliated sensory pits present dorsolaterally; intestine level muscle ring absent; (Fig. 5.14 E) ..... *Microstomum*

Platyhelminthes: Lecithoepitheliata: Prorhynchidae: Genera

Body elongate with rounded or widened anterior end, with posterior end pointed or truncated. Pigmentation whitish-yellowish, sometimes brownish. Pharynx plicatus or variabilis. Brain ovoid without lobes. Eyes absent. Oral and genital pores usually common. Ciliated pits sometimes present. Statocyst or refractile organs absent. Asexual reproduction absent. Testes follicular. Sclerotic structures (stylet) present and below the pharynx located. Orientation of male organ frontally or caudally. Ovary or female gonads diffuse apparently without tunica propia, germinal and yolk cells together (ovovitellar).

1 Body shape elongate with rounded or widened anterior end, posterior end pointed or rounded; pharynx tubular bulbous; eyes absent; stylet straight, mucronate 2

1′ Body shape elongate with anterior end explanate, posterior end rounded; pharynx bulbous, spindle-like; eyes present; stylet infundibuliform and curved; (Fig. 5.14 F) ..... *Geocentrophora*

2(1) Ciliated pits present; female and male gonopore common; testes paired; orientation of male organ caudal, stylet separate from the male apparatus and differentiated as venom organ; (Fig. 5.14 G) ..... *Xenoprorhynchus*

2′ Ciliated pits absent; female and male gonopore separate; testes follicular; orientation of male organ anterior; stylet forms part of the male copulatory organ; (Fig. 5.14 H) ..... *Prorhynchus*

Platyhelminthes: Catenulida: Families

Body elongate with rounded or width anterior end (prostomium) and posterior end pointed or truncated. Frequently anterior end (prostomium) separated from the rest of the body by a ciliated furrow. Pigmentation whitish to yellowish. Pharynx simplex. Brain with anterior and posterior lobes. Eyes absent. Oral and genital pores separated. Oral pore ventral and genital pore dorsal. Ciliated pits, statocyst, and refractile organs present. Asexual reproduction present, commonly with asexual reproduction via paratomy (production of characteristic zooid chains). Testes follicular. Sclerotized male structures as stylet present. Orientation of male organ frontally. Ovary or female gonads ovary and vitellaria fully separated.

1 Body shape elongate with ciliated furrow and prostomium present; brain ovoid without anterior lobes; without paired refractile organs; male pore dorsally behind or before oral pore 2

1′ Body shape elongate with only a ventral ciliated furrow present, prostomium absent; brain ovoid with anterior and posterior lobes; paired refractile organs near posterior brain lobes; dorsal male pore at level of oral pore ..... **Stenostomidae**

2(1) Anterior ciliated pits present; statocyst present; gut without excretophores; male pore posterior to oral pore; with two or more (multiple) zooids ..... **Catenulidae**

2′ Anterior ciliated pits absent; statocyst absent; gut with excretophores; male pore anterior to oral pore; with two or at most three zooids; (Fig. 5.15 A) ..... Chordariidae, one species: *Chordarium europaeum* Schwank, 1980

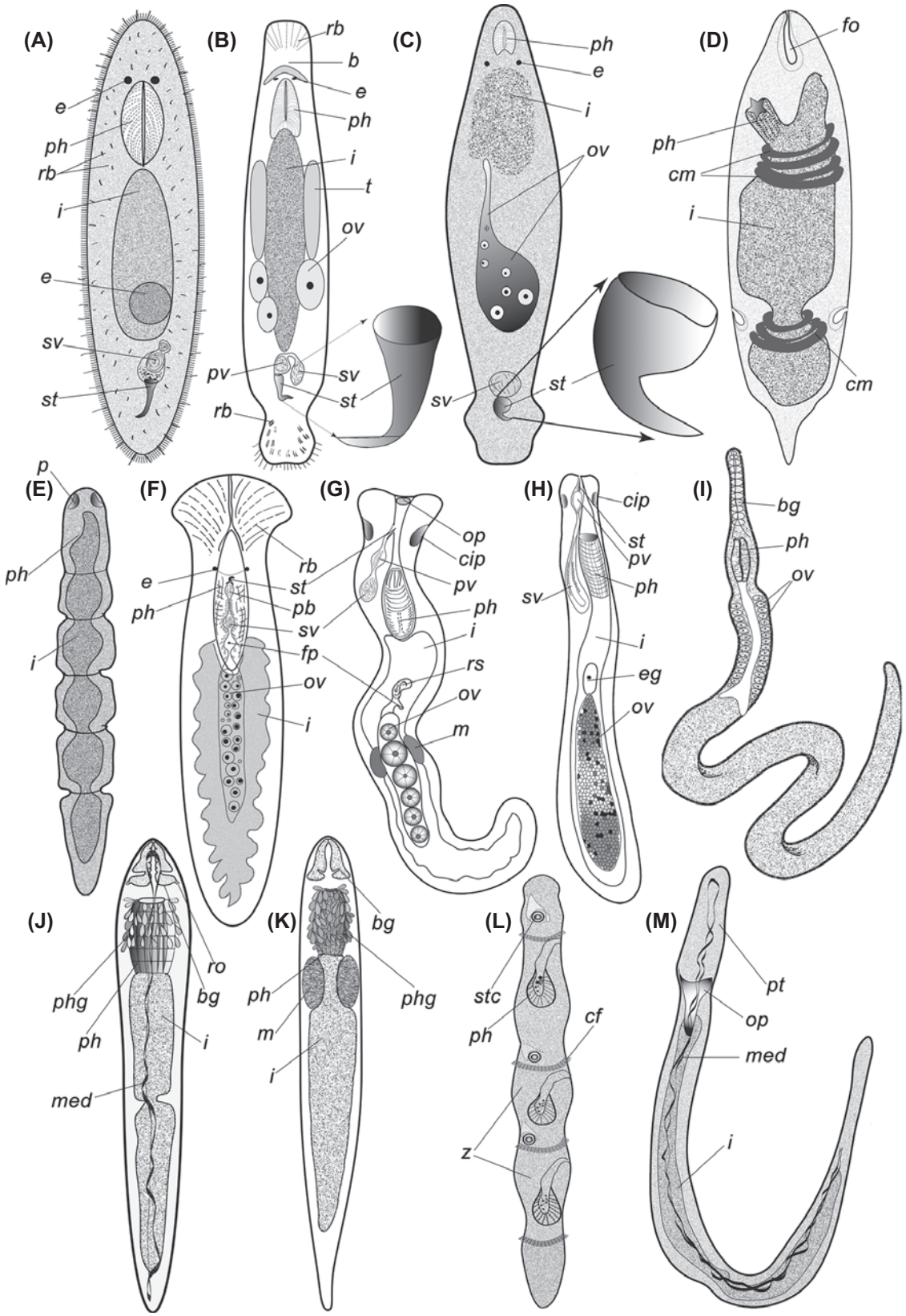


FIGURE 5.14 Macrostomidae, Macrostomida: (A) *Promacrostomum*; (B) *Macrostomum*; (C) *Omalostomum*. Microstomidae, Macrostomida (D) *Myozonella*; (E) *Microstomum*. Prorynchidae, Rhabdocoela: (F) *Geocentrophora*; (G) *Xenorhyunchus*; (H) *Prorhynchus*. Stenostomidae, Catenulida: (I) *Rhynchoscolex*; (J) *Stenostomum*; and (K) *Myostenostomum*; Catenulidae, Catenulida: (L) *Catenula*; (M) *Dasyhormus*.

Platyhelminthes: Catenulida: Stenostomidae: Genera

Statocysts absent. Usually paired refractile organs near the posterior brain lobes. Gut with excretophores present. Zooid chains normally with two or at most three zooids.

1	Anterior end rounded; with or without anterior brain lobes; with anterior ciliated pits; excretophores in an irregular or disordered arrangement 2
1′	Anterior end elongate, probosciform; multiple anterior brain or ganglia lobes; without anterior ciliated pits; refractile organs absent; gut with regularly arranged excretophores; male pore absent (after Luther, 1960); (Fig. 5.14 I) ..... *Rhynchoscolex*
2(1)	Paired refractile organs between posterior brain lobes and pharynx (not in all species); muscular bulb between pharynx and intestine absent; brain with one pair of posterior lobes and multilobes anteriorly; (Fig. 5.14 J) ..... *Stenostomum*
2′	Paired refractile organs between posterior brain lobes and pharynx absent; muscular bulb between pharynx and intestine present; brain with one pair of anterior and posterior lobes; (Fig. 5.14 K) ..... *Myostenostomum*

Platyhelminthes: Catenulida: Catenulidae: Genera

Statocyst present. Paired refractile organs behind the posterior brain lobes absent. Gut excretophores absent. Asexual reproduction via chain of zooids with two or more (multiple) zooids.

1	Prostomium normal; brain ovoid with two posterior lobes; statocyst present; gut with excretophores absent; (Fig. 5.14 L) ..... *Catenula*
1′	Prostomium short and rounded; brain ovoid without lobes; statocyst absent; gut with excretophores present; (Fig. 5.14 M) ..... *Dasyhormus*

Platyhelminthes: Prolecithophora: Families

Body elongate with rounded or widened anterior end, posterior end pointed or truncated. Pigmentation variable, reddish or whitish, in some species with stripes. Pharynx plicatus or variabilis. Brain ovoid without posterior or anterior lobes. Eyes usually present. Oral and genital pore separated. Ciliated pits, statocyst or refractile organs absent. Testes follicular. Sclerotic male structures, like a stylet, present. Orientation of male organ frontally. Ovary or female gonads diffuse apparently without tunica propia, germinal and yolk cells together (ovovitellar).

1	Body elongate with anterior end rounded; eyes present; oral and genital pore openings separate 2
1′	Body elongate with anterior end truncate and posterior end acute; eyes absent; oral and genital pores open together in a common pore; stylet present ..... **Protomonotresidae**
2(1)	Coloration opaque, greenish to yellowish, with pigmented stripes; pharynx variabilis (or plicatus); sexual reproduction organs single; testes dorsal and follicle-shaped; without sclerotized structures on the male organs; (Fig. 5.15 G) ..... Plagiostomidae, one genus: *Plagiostomum*
2′	Coloration reddish; pharynx plicatus; sexual reproduction organs multiple; testes paired, posterior to female tissue; male organs armed with a cirrus; (Fig. 5.15 H)..... Multipeniatidae, one species: *Multipeniata kho* Nasonov, 1927

Platyhelminthes: Prolecithophora: Protomonotresidae: Genera

Body elongate with anterior end truncate and posterior end acute. Pigmentation opaque, greenish to yellowish, with oil drops. Pharynx plicatus. Brain ovoid without anterior lobes. Eyes absent. Oral and genital pores open together in a common pore. Ciliated sensory pits, refractile organs or statocyst absent. Sexual reproduction organs single, not paired. Testes dorsal and follicular. Sclerotic male structures (such as a stylet) present. Asexual reproduction absent. Orientation of male stylet anterior. Female gonads diffuse apparently without tunica propia, germinal and yolk cells together (ovovitellar).

1	Body elongate or clavate 2
1′	Body elongate with anterior and posterior end acute 4
2(1)	Unpigmented; sclerotic male structures absent; ovary or female gonads irregular, germinal and yolk cells fully separated 3
2′	Pigmentation yellowish with oil drops or greenish; stylet present; ovary or female gonads diffuse apparently without tunica propia, germinal and yolk cells together (ovovitellar); (Fig. 5.15 B) ..... *Protomonotresis*
3(2)	Oral and genital pores common; (Fig. 5.15 C) ..... *Porfirievia*
3′	Oral and genital pores separated; (Fig. 5.15 D) ..... *Baicalarctia*
4(1)	Pigmentation yellowish with oil drops or greenish; ovary or female gonads diffuse apparently without tunica propia, germinal and yolk cells together (ovovitellar); oral and genital pore common; (Fig. 5.15 E) ..... *Archimonotresis*
4′	Pigmentation unpigmented; ovary or female gonads irregular, germinal and yolk cells fully separated; oral and genital pores separated; (Fig. 5.15 F) ..... *Friedmaniella*

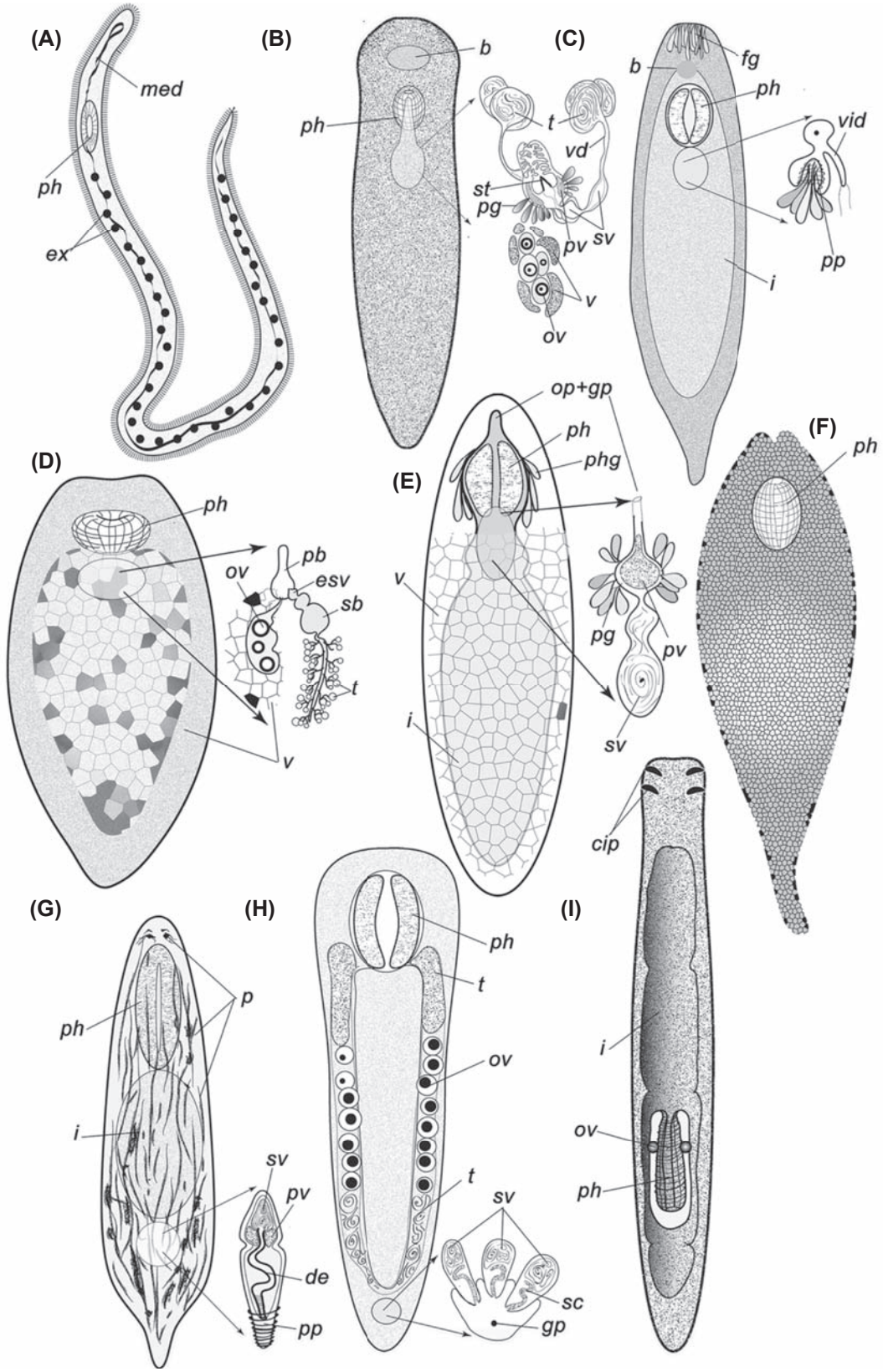


FIGURE 5.15 Chordiidae, Catenulida: (A) *Chordarium*. Protomonotresidae, Prolecithophora: (B) *Protomonotresis*; (C) *Porfirievia*; (D) *Baicalarctia*; (E) *Archimonotresis*; (F) *Friedmaniell(A)* Plagiostomidae, Prolecithophora: (G) *Plagiostomum*. Multipeniatidae, Prolecithophora: (H) *Multipeniat(A)* Bothrioplanidae, Bothrioplanida; and (I) Bothrioplana.

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Chapter 6

Phylum Nemertea

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INTRODUCTION

There are around 1275 described nemertean species (Kajihara et al. 2008), with the vast majority being marine, and only 22 species are currently known from freshwater habitats. Most freshwater species, 14 species in five genera, are known from the Palearctic region. It is, however, important to emphasize that this probably reflects sampling efforts rather than true geographic distribution of freshwater species. Historically, there is a clear predominance of taxonomists who are interested in nemerteans from this region rather than other regions, and this may introduce bias in the distribution of species. Two species are hitherto known as endemic in the Palearctic region: *Amniclineus zhujiangensis* Gibson & Qi, 1991 and *Limnemertes poyangensis* Gibson & Wang, 2002. The freshwater nemerteans of Palearctic are all benthic, like all other known freshwater species. Being often overlooked, the ecological impact of these species is unknown.

LIMITATIONS

The number of freshwater nemertean species is certainly underestimated, and genetic evidence shows that sibling and cryptic species are more common than previously recognized. There is no universal agreement on the actual number of genera and species, but current figures indicate that the classes Palaeonemertea and Pilidiophora account for approximately 38% of the known genera and 44% of the named species, and Hoplonemertea for 62% of genera and 56% of species. The number of known freshwater nemerteans is small; the 22 reported species represent less than 2% of the total number recorded. The current knowledge of freshwater species is that no palaeonemerteans are found in these habitats (for overview see Sundberg & Gibson, 2008).

Only adult nemerteans possess the morphological characters reflected in the identification key. Juveniles are in most cases not possible to identify with confidence. Some Palearctic species can be roughly identified by a combined knowledge of shape, size, and color (and, of course, sampling site).

The genus *Prostoma* is confused and in need of revision. Most descriptions accompanying occurrences that have been recorded are either incomplete or uninformative. Many authors appear either to have assumed that their material belonged to one *Prostoma* species, or erect new species on the basis of characters subsequently shown to have no taxonomic value.

TERMINOLOGY AND MORPHOLOGY

A variety of details are required to identify freshwater nemerteans. The first things to look for are the cephalic slits, located on the sides of the head, which are present only in Heteronemertea. If cephalic slits are lacking, there can be cephalic furrows (Hoplonemertea) most often

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located on the dorsal side of the head. It is also important to observe the presence or absence of eyes, number and eye placement pattern (if present), and body color.

MATERIAL PREPARATION AND PRESERVATION

Nemerteans should be examined alive whenever possible; and for identification, a stereo microscope is often needed. For histological sections, anesthetize the animal with MS 222 or $MgCl_2$ before fixation to minimize contractions (which will distort anatomical characters). Common fixatives for nemerteans are Bouin's fluid or 3%–4% formalin. Ethanol is required for DNA extractions but is less suitable for histology. Another good fixative for RNA and DNA studies is RNAlater, which is easy to transport (being neither toxic nor flammable) and especially suited for fieldwork. Freeze specimens for molecular analysis.

Refer to general textbooks and manuals for histological techniques and embedding specimens in paraffin.

KEYS TO NEMERTEA

The phylum is divided into three the classes (Strand et al 2018): Palaeonemertea, Pilidiophora (including Heteronemertea) and Hoplonemertea (stylet-bearing proboscis). Freshwater nemerteans are only known from the Heteronemertea and Hoplonemertea.

Nemertean Classes

1	Head with cephalic slits (Fig. 6.1)	**Heteronemertea**
1′	Head without cephalic slits	**Hoplonemertea**

Nemertea: Heteronemertea: Species

1	Reddish, no spots	2
1′	Brick red, speckled with numerous white spots	*Apatronemertes albimaculosa* Wilfert & Gibson, 1974 (Germany [only known from aquaria at the Düsseldorf City Aquarium])
2(1)	Rose red, 2–4 cm long, 1–2 mm wide	*Amniclineus zhujiangensis* Gibson & Qi, 1991 [China]
2′	Scarlet or purplish red, 4–14 cm long, 2–5 mm wide	*Yininemertes pratensis* Sun & Lu, 1998 [China]

Nemertea: Hoplonemertea: Species

Prostoma includes small slender monostiliferous hoplonemerteans with shallow and often indistinct horizontal longitudinal cephalic grooves. Body coloration varies in the genus, including shades of cream, yellow, gray, pink, brown, red, and orange; some individuals are flecked or speckled in deeper shades. Juveniles are invariably white, pale yellow, or cream. Adult body coloration deepens with age to shades of reds, oranges, and browns. Body coloration may furthermore depend on the diet. It is therefore not possible to distinguish *Prostoma* species on the basis of color or other external characters except the two species lacking eyes.

1	Four to eight eyes	2
1′	No eyes	*Prostoma* [Widespread]



FIGURE 6.1 Lateral cephalic slit in a freshwater nemertean.

2(1)	Body greenish	*Limnemertes poyangensis* Gibson & Wang, 2002 [China]
2′	Adults reddish brown	*Prostoma* [Widespread]

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Chapter 7

Phylum Gastrotricha

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INTRODUCTION

The phylum Gastrotricha includes over 830 free-living species widespread in marine, brackish, and freshwater ecosystems (Balsamo et al., 2013, 2014). These animals represent a quantitatively significant component of the meiobenthic fauna although they are still poorly known. The phylum is divided into two orders, Macrodasyida and Chaetonotida, which are very different in morphology, biology, and ecology (Remane, 1936) (Fig. 7.1). Macrodasyida number over

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360 species, with all but two being marine or estuarine. Freshwater habitats are colonized almost exclusively by Chaetonotida, comprising over 470 species overall, most of which (~340) live in inland waters, and are heterogeneously distributed (Balsamo et al., 2013). Most freshwater gastrotrichs are epibenthic, periphytic, or semiplanktonic in eutrophic, lentic habitats. Only a few interstitial species colonize sediments in lotic or brackish waters, and then only in low numbers (Ricci & Balsamo, 2000). Gastrotricha are a minor, but ecologically important, phylum in inland water environments, since they are a component of the microphagous, detritivorous zoobenthic community, and represent a basic link between the microbial loop and the higher trophic levels. Some marine and freshwater species have been proven to be valuable bioindicators (Balsamo & Todaro, 2002).

LIMITATIONS

Current knowledge of freshwater Gastrotricha is mainly based on data from the Palearctic. This has been by far the most studied biogeographical region for gastrotrichs due to the numbers of researchers in this region. At present, the freshwater gastrotrich fauna from Palearctic includes about 235 species of Chaetonotida and a single species of Macrodasyida.

Identification of Palearctic freshwater Gastrotricha is relatively simple to genus level, since generic diagnostic characters are generally clear and well defined. Genus level identification requires a careful microscopical examination of adult specimens, alive if possible.

In contrast, species identification is very difficult due to the extremely fine details required to distinguish close taxa, and the great range of intraspecific variability. Moreover, undescribed species are still being discovered. Specific identification is much more problematic due to the uncertain boundaries between numerous, closely related species. This is particularly true for *Chaetonotus*, the largest genus, which needs revision. It must be emphasized that species-level taxonomy, especially for freshwater species, is unsatisfactory and unstable because: (1) many original descriptions date back to the nineteenth and early twentieth centuries and are often ambiguous, insufficient, vague and quite far from modern standards; and (2) the morphological intraspecific variability of numerous species has led to the taxonomy being somewhat discretionary as regards to maintaining some original taxa or splitting them into separate taxa.

Freshwater Gastrotricha literature is mostly composed of single species descriptions. Some "regional" faunas or extensive papers containing identification keys have been published and may be useful in species identification: Rudescu (1967), Roszczak (1969), d'Hondt (1978), Balsamo (1983), Schwank (1990), Kisielewki (1991, 1997, 1998), Balsamo & Todaro (2002), Balsamo et al. (2009, 2014), and Kånneby et al. (2009). Data on taxonomy and geographical distribution of freshwater species are also available on the databases of Fauna Europaea, FADA, and WoRMS.

TERMINOLOGY AND MORPHOLOGY

Gastrotricha are bilateral, transparent, vermiform, or fusiform micrometazoans, ranging in body length from less than 100 μm to over 3 mm. They actively crawl or swim by an extensive ventral **ciliature**, and can temporarily anchor to the substrate by two to four **caudal (furcal) adhesive tubes**. The general body shape and proportions, the outline of the head (depending on the presence and size of protective **cephalic plates**), the shape and size of the caudal end (in particular the **adhesive tubes**), the surface aspect of the **cuticle** (often with various external elements such as scales, spines, or plates) are all features of basic taxonomic importance. The strongly muscularized **pharynx** has a **triradiate lumen** oriented differently in Macrodasyida and Chaetonotida, respectively; the shape of the pharynx is a diagnostic feature but it must be observed *in vivo* since it may be altered after death.

Freshwater species are parthenogenic. The ratio between the length of full-grown oocytes and the body length of Chaetonotida, up to 1:3, is among the largest known in the Animal Kingdom, and the silhouette of the mature animal is greatly deformed. Two kinds of eggs are produced, **quick hatching** and **late hatching**, which can be distinguished by external morphology. The first are transparent and the developing embryo can be observed inside, while the second have a much thicker, dark envelope and appear matte.

The so-called **X-organ** can be occasionally seen in adult specimens. This compact, clearly visible, horseshoe-shaped organ surrounding the terminal intestine is probably related to a postparthenogenic, hermaphroditic phase of the biological cycle, during which few, rudimentary spermatozoa may appear at both sides of the intestine. The shape and size of these vestigial spermatozoa is various and species specific, and may be specific diagnostic characters.

MATERIAL PREPARATION AND PRESERVATION

Gastrotricha are more successfully studied alive, since their frailty and strong contractility generally cause alterations of the diagnostic characters. Small amounts of sediment (2–3 cm^3) are picked up one at a time from the sample using a bulb syringe, transferred to small Petri dishes (10 cm in diameter) and directly examined under the stereomicroscope. Adding a 4% aqueous solution of $MgCl_2$ to the water causes the temporary immobilization of the specimens and makes their extraction easier, especially from sandy sediments. Single individuals are isolated by picking them up with a micropipette and transferring them to small vials containing filtered water for subsequent study.

Samples for quantitative analyses as well as samples that cannot be examined in a short time must be treated *in toto* with fixative immediately after collection. In these cases, a prior treatment of the entire sediment sample with a

2% aqueous solution of $MgCl_2$ is necessary for separating animals from the sediment to prevent possible distortion effects. After slowly mixing sediment and liquid for several minutes, 10% neutralized formalin is added to the volume of the liquid present in the sample (ratio 1:1) so that the final concentration of fixative is 4%–5%.

The extraction of all the specimens from a preserved sample is clearly critical for quantitative analyses, but regrettably the techniques currently available are not satisfactory for gastrotrichs. Density gradient centrifugation is the most effective method (Giere, 2009).

Single, isolated specimens are mounted on slides in a water drop. A clean small coverglass (≤15 mm) is gently placed on the drop after its corners have been slightly scraped on a block of plasticine so that the coverglass is slightly raised above the slide. This avoids excessive compression of the specimen. A living gastrotrich moves quickly, and once mounted on a slide it can be slowed down by slight pressure on the coverglass, and by gradually absorbing some water from the side of the coverglass with a thin strip of blotting paper. If the examination is prolonged, the specimen may be previously anesthetized by adding a drop of 1%–1.5% $MgCl_2$ or a very dilute solution of an alkaloid-like procaine; then it can be mounted in a drop of the same anesthetic solution. Anesthetized specimens can be fixed during examination by adding some drops of 4% neutralized formalin. An alternative fixative, effective for ultrastructural study, is a mixture of paraformaldehyde and glutaraldehyde in 0.1 M cacodylate buffer, in a saturated solution of picric acid (PAFG, Ermak & Eakin, 1976). Since this mixture is very stable even at room temperature, it will keep stored specimens for long periods. Single fixed specimens can be mounted in permanent slides for archive; in this case, the coverglass is sealed with Glyceel or several layers of nail polish.

For scanning electron microscopy (SEM), fixed specimens are repeatedly rinsed in phosphate bufferred saline or cacodylate buffer (pH 7.4), and then dehydrated in an ethanol or an acetone graded series (25%–100%), for at least 10 min each passage; the last two passages (95%, 100%) must be repeated twice. Specimens can then be processed by Critical-Point Drying (CPD) using CO_2, according to a protocol suitable for delicate biological samples such as described by Luporini & Tongiorgi (1972). An alternative preparation is a chemical drying using hexamethyldisilazane (HMDS) (Hochberg & Litvaitis, 2000). This method is very rapid and is especially useful when only a few and/or very small specimens have to be prepared, when the risk of losing them during the CPD process is very high. Once dried, the specimens are picked up one by one through a very thin hair with a handle, then laid on an aluminum SEM support and immediately coated with a conductive, metallic layer in a sputtering metalizer system. Treated specimens are highly hygroscopic and must be kept in a vacuum dryer chamber until they are observed under the electron microscope.

Considering the limited usefulness of permanent slides, which generally deteriorate over time, the value of documentation is very high. Photomicrographs and/or videos of living and/or fixed specimens are of basic importance and are routinely taken to complement the other data obtained from microscopical examination. Because some characters are only visible in living specimens (e.g., arrangement of sensory ciliature, structure of reproductive system) microphotography and video recording are essential.

KEYS TO GASTROTRICHA

Gastrotricha: Orders

1 Body vermiform, 200 µm to 3 mm long; few to many anterior and caudal adhesive tubes, possibly laterally also; smooth or sculptured body cuticle, two pharyngeal pores; hermaphroditic with complex reproductive system, sporadically parthenogenic (Figs. 7.1 A and 7.2). Marine, brackish water, two freshwater genera; interstitial ..... Macrodasyida, one species: *Marinellina flagellata* Ruttner-Kolisko, 1955 [Austria]

1′ Body fusiform, 80–400 µm; only two (rarely four) caudal adhesive tubes forming the "furca"; smooth or sculptured body cuticle; no pharyngeal pores; hermaphroditic with simple reproductive system, mostly parthenogenic (Figs. 7.1 B, C). Marine, brackish, mostly freshwater; epibenthic, interstitial, or semiplanktonic; 235 freshwater species from Palearctic ..... **Chaetonotida**

Gastrotricha: Chaetonotida: Families

1 Furcal appendages reduced or absent; body cuticle bare or very thinly sculptured; semiplanktonic or planktonic 2

1′ Furcal appendages present, each made of 1–2 well-developed adhesive tubes; body cuticle scaled and/or spined, rarely bare; epibenthic, periphytic, or interstitial 3

2(1) One paired clavate, cephalic tentacle; no ventrolateral motile spines; body cuticle thinly scaled and spined; freshwater, semiplanktonic or planktonic (Figs. 7.3–6) ..... **Neogosseidae**

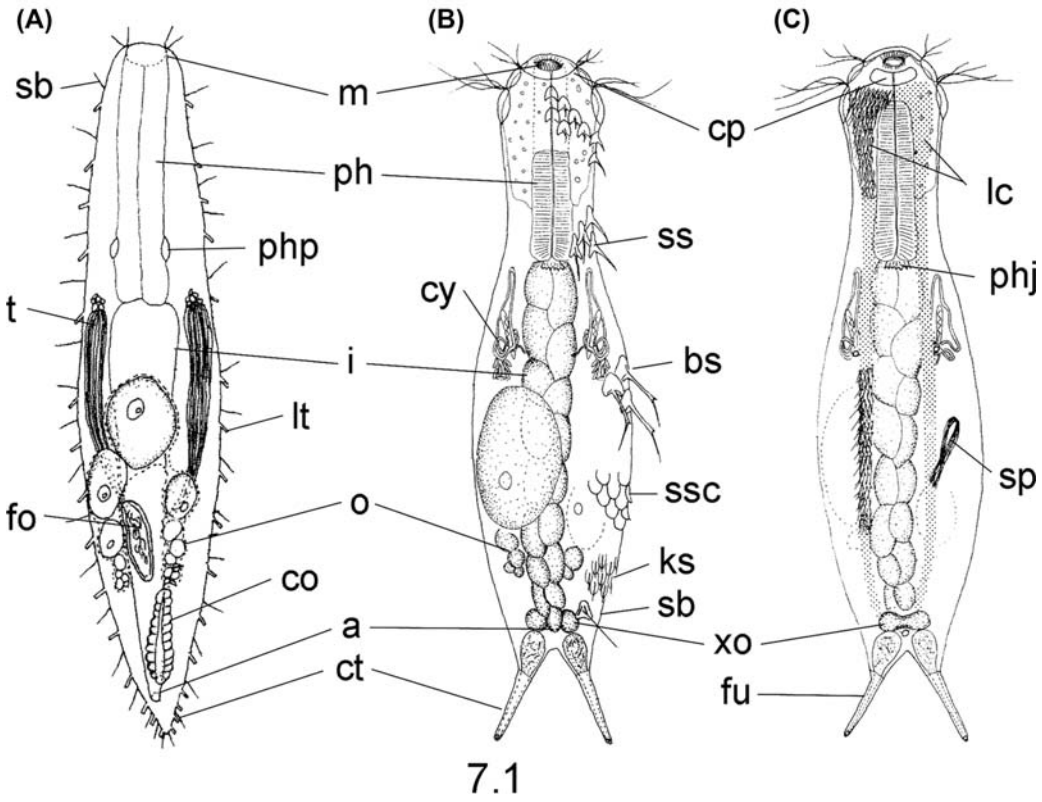


PLATE 1 Fig. 7.1 Scheme of the anatomy of a Macrodasyida (A) and of a Chaetonotida gastrotrich from a dorsal (B) and a ventral (C) view. *a*, anus; *bs*, scale with barbed spine; *co*, caudal organ; *cp*, cephalic plates; *ct*, caudal adhesive tubes; *cy*, cyrtocyte; *fo*, frontal organ; *fu*, furca; *i*, intestine; *ks*, keeled scales; *lc*, locomotory ciliature; *lt*, lateral adhesive tubes; *m*, mouth; *o*, ovary; *ph*, pharynx; *phj*, pharyngeal-intestinal junction; *php*, pharyngeal pore; *sb*, sensory bristle; *sp*, vestigial spermatozoa; *ss*, scale with simple spine; *ssc*, smooth scale; *t*, testis; *xo*, X-organ. (Modified from Balsamo & Todaro, 2002 with permission).

2′	No cephalic tentacles; ventrolateral groups of very long, often motile spines; body cuticle smooth or very finely scaled; freshwater, semiplanktonic or planktonic (Figs. 7.7–27) ..... **Dasydytidae**
3(1)	Each furcal appendage made of one adhesive tube; body cuticle usually sculptured (scales, spines). Marine, brackish water, mostly freshwater epibenthic, periphytic, interstitial 4
3′	Each furcal appendage made of two adhesive tubes; body cuticle bare; freshwater, epibenthic; very rare (Figs. 7.28–31) .... Dichaeturidae, one genus: ***Dichaetura***
4(3)	Stout, curved, diverging adhesive tubes; cephalic ciliature not arranged in tufts: cephalic plates absent; very small body apparently covered with transparent, undulate membranes.; three paired dorsal sensory bristles on the head, on the neck, and at the furca base; freshwater, epibenthic or hyperbenthic; very rare (Fig. 7.32) ..... Proichthyidiidae, one species: *Proichtydioides remanei* Sudzuki, 1971 [Japan]
4′	Straight adhesive tubes; cephalic ciliature arranged in tufts; cephalic plates present; marine, brackish water and freshwater; epibenthic, periphytic, and interstitial; very common (Figs. 7.33–35) ..... **Chaetonotidae**

Gastrotricha: Chaetonotida: Neogosseidae: Genera

1	Body end truncated; two stout, possibly claw-like, caudal protuberances with a paired group of long spines; body cuticle finely scaled and spined; four pharyngeal bulbs (Figs. 7.3–5) ..... ***Neogossea***
1′	Body end rounded; one unpaired, median group of short spines; body cuticle scaled on the neck and trunk, occasionally bare except one paired small ventral scaled area; 1–2 pharyngeal bulbs (Fig. 7.6) .... *Kijanebalola*, one species: *Kijanebalola dubia* de Beauchamp, 1932 [United Kingdom (?) Afrotropical]

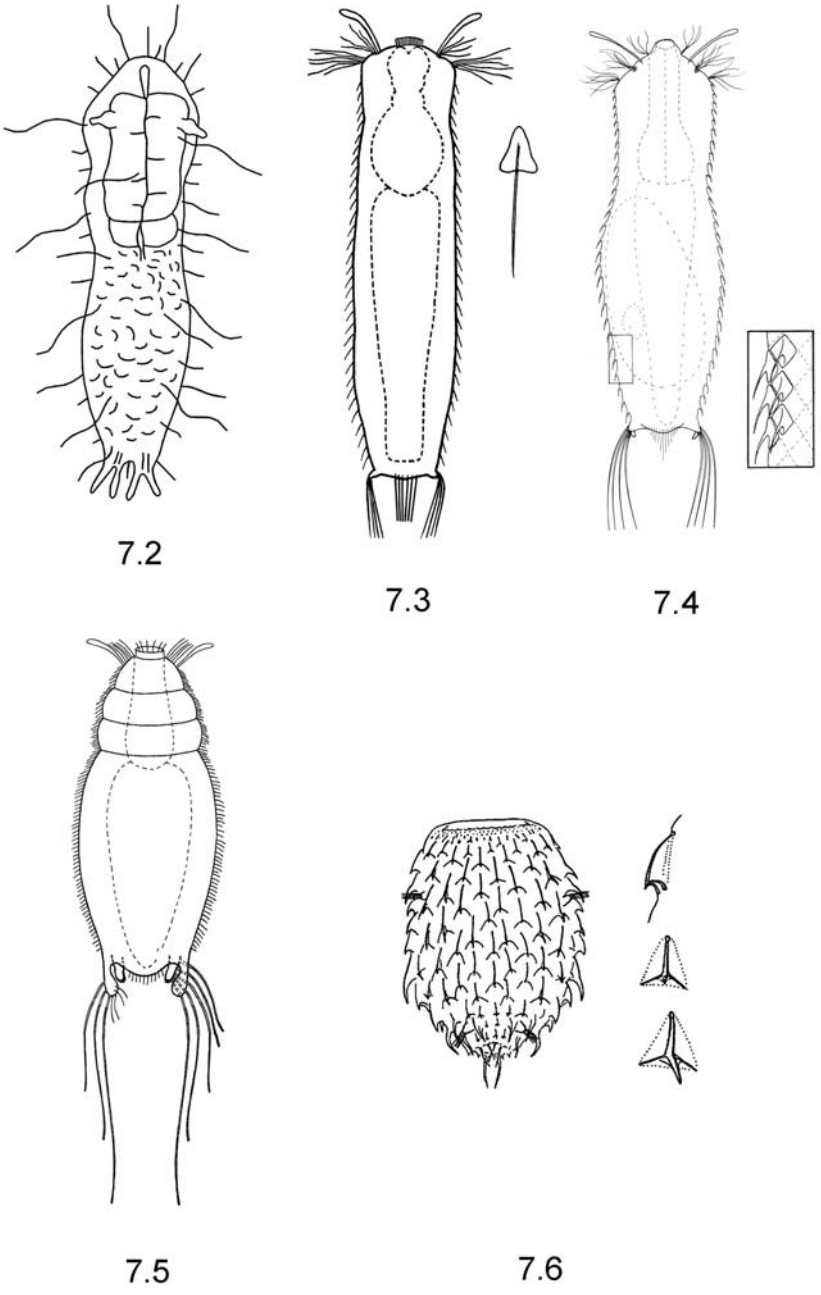


PLATE 2 Fig. 7.2 *Marinellina flagellata* (Macrodasyida, *incertae sedis*): dorsal view (redrawn from Ruttner-Kolisko, 1955); Fig. 7.3 *Neogossea voigti* (Daday, 1905): dorsal view with a detail of a scale (from Kisielewski, 1974 with permission); Fig. 7.4 *Neogossea antennigera* (Gosse, 1851): dorsal view with a detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.5 *Neogossea fasciculata beauchampi* d'Hondt, Pourriot, Rougier, & Guiral, 2005: dorsal view: the caudal end is shown dorsally on the left and ventrally on the right side (redrawn from Daday, 1905); Fig. 7.6 *Kijanebalola dubia* de Beauchamp, 1932: dorsal view with detail of scales (from de Beauchamp, 1932).

Gastrotricha: Chaetonotida: Neogosseidae: *Neogossea*: Species

1	Caudal appendages unguiform	2
1′	Caudal appendages rounded (Fig. 7.3)	*Neogossea voigti* Daday, 1905 [Germany, Poland, Romania, United Kingdom]
2(1)	Small, unguiform caudal appendages, each with a group of caudal spines (Fig. 7.4)	*Neogossea antennigera* (Gosse, 1851) [Austria, Italy, Poland, Romania, Russia, United Kingdom]
2′	Well-developed, unguiform, bilobate caudal appendages, each with two groups of caudal spines (Fig. 7.5)	*Neogossea fasciculata beauchampi* d'Hondt, Pourriot, Rougier, & Guiral, 2005 [France, Poland, Romania]

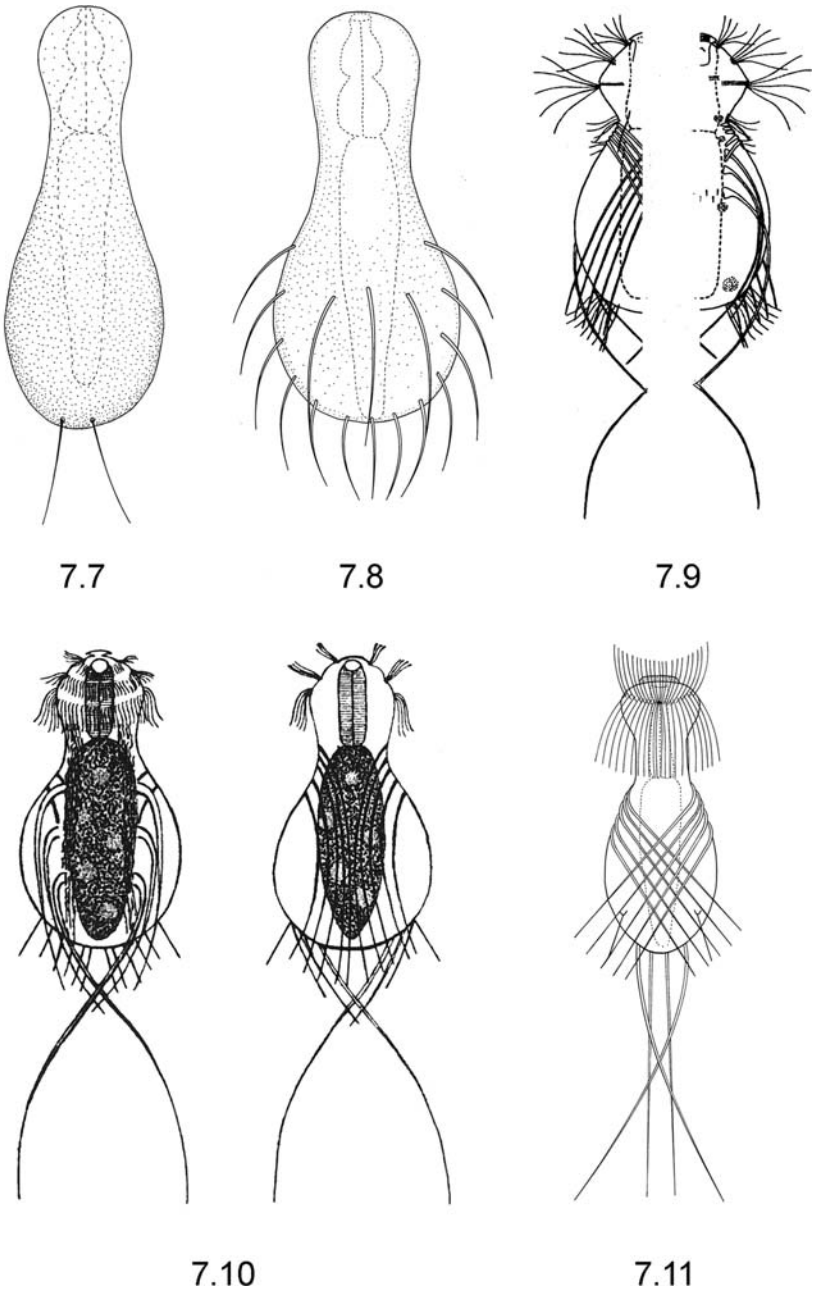
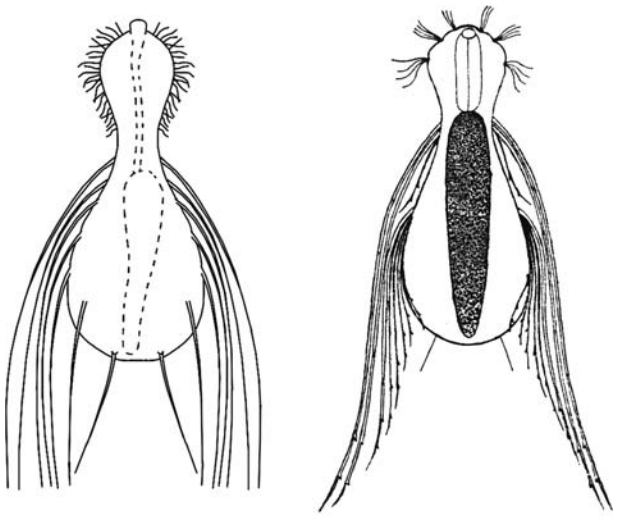


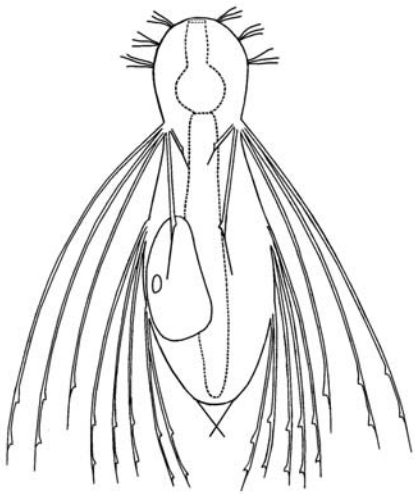
PLATE 3 Fig. 7.7 *Anacanthoderma punctatum* Marcolongo, 1910: dorsal view (from Balsamo, 1983 with permission); Fig. 7.8 *Anacanthoderma paucisetosum* (Marcolongo, 1910): dorsal view (from Balsamo, 1983 with permission); Fig. 7.9 *Haltidytes festinans* (Voigt, 1909): schematic composition of dorsal view (*left*) and ventral view (*right*) (redrawn from Kisielewski, 1991); Fig. 7.10 *Haltidytes crassus* (Greuter, 1917): ventral and dorsal views (from Greuter, 1917); Fig. 7.11 *Haltidytes saltitans* (Stokes, 1887): dorsal view (from Balsamo, 1983 with permission).

Gastrotricha: Chaetonotida: Dasydytidae: Genera

1	Body fusiform, elongate or bottle-shaped; caudal end rounded or truncated; cuticle with keeled/spined scales; no dorsal spines; numerous ventrolateral and caudal spines long to very long; pharynx cylindrical or with a small posterior bulb 2
1′	Body bottle-shaped with rounded caudal end; cuticle smooth or with several dorsal long, simple spines; no ventrolateral spines; pharynx with two bulbs; rare (Figs. 7.7 and 8) ..... ***Anacanthoderma***
2(1)	Body end rounded with two short bristles, or truncated with two stout protuberances bearing 2–3 short bristles; no ventrolateral "saltatory" spines 3



7.12 7.13



7.14

PLATE 4 Fig. 7.12 *Chitonodytes longisetosus* (Metschikoff, 1865): dorsal view (from Balsamo, 1983 with permission); Fig. 7.13 *Chitonodytes longispinosus* (Greuter, 1917): dorsal view (modified from Greuter, 1917); Fig. 7.14 *Chitonodytes collini* (Remane, 1927): dorsal view (modified from Remane, 1927).

2′	Body end rounded often with two long, simple spines; body cuticle smooth; two ventrolateral very long, simple, flexible, "saltatory" spines, intersecting over the trunk in the resting position (Figs. 7.9–11) ..... ***Haltidytes***
3(2)	Body end rounded or truncated with two elongate protuberances; usually ventrolateral very long spines extending beyond the caudal end and adhering to the body in the resting position; spines often spreadable; cylindrical pharynx or with a posterior bulb 4
3′	Body end truncated with two short, conical protuberances, each bearing a long spine; several ventrolateral long, thick, simple or barbed spines, single or in groups; spines not motile, never reaching half the length of the body; cylindrical pharynx 5
4(3)	Bottle-shaped body; caudal end rounded with two bristles; lateral spines usually double barbed, single or in groups (Figs. 7.12–14) .... ***Chitonodytes***
4′	Fusiform or elongate body; caudal end truncated with two elongated protuberances, each with 2–3 short bristles (*styli*); usually lateral long, barbed spines arranged into groups (Figs. 7.15–18) ..... ***Stylochaeta***
5(3)	Slender body; up to more than 50 lateral, barbed, very long spines, single or in groups (up to nine groups) (Figs. 7.19–21) .... ***Dasydytes***
5′	Fusiform body; up to 12 lateral, simple or barbed spines of medium length, single or in groups (up to five groups) (Figs. 7.22–27) .... ***Setopus***

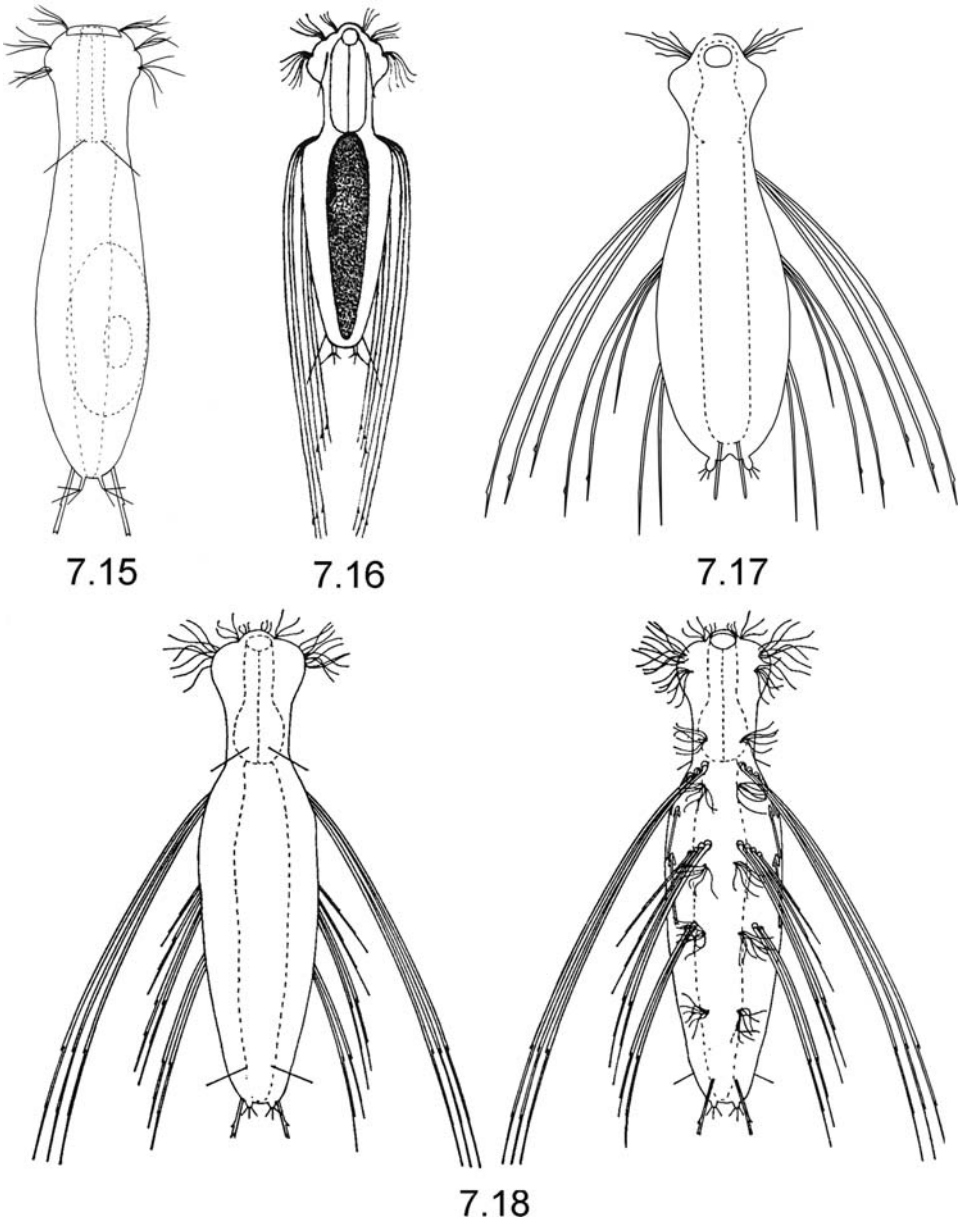


PLATE 5 Fig. 7.15 *Stylochaeta stylifera* (Voigt, 1901): dorsal view (from Balsamo, 1983 with permission); Fig. 7.16 *Stylochaeta longispinosa* Greuter, 1917: dorsal view; Fig. 7.17 *Stylochaeta scirtetica* Brunson, 1950: dorsal view (modified from Brunson, 1950); Fig. 7.18 *Stylochaeta fusiformis* (Spencer, 1890): dorsal and ventral views (from Balsamo, 1983 with permission).

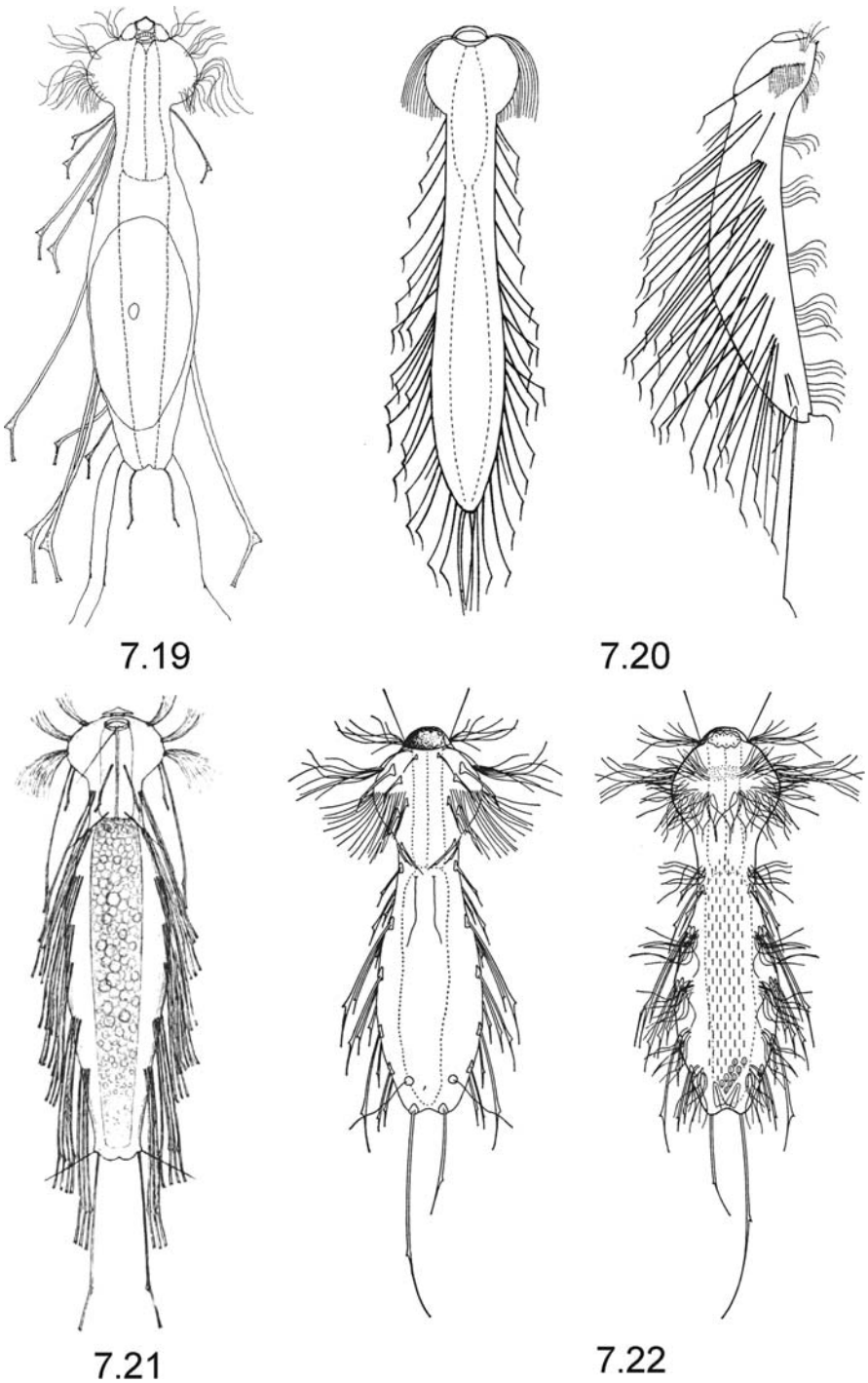


PLATE 6 Fig. 7.19 *Dasydytes (Dasydytes) asymmetricus* Schwank, 1990: dorsal view (from Schwank, 1990 with permission); Fig. 7.20 *Dasydytes (Dasydytes) goniathryx* Gosse, 1851: dorsal and lateral views with detail of a spine (modified from Rudescu, 1967); Fig. 7.21 *Dasydytes (Dasydytes) ornatus* Voigt, 1909: dorsal view (modified from Voigt, 1909); Fig. 7.22 *Setopus tongiorgii* (Balsamo, 1983): dorsal and ventral views (from Balsamo, 1983 with permission).

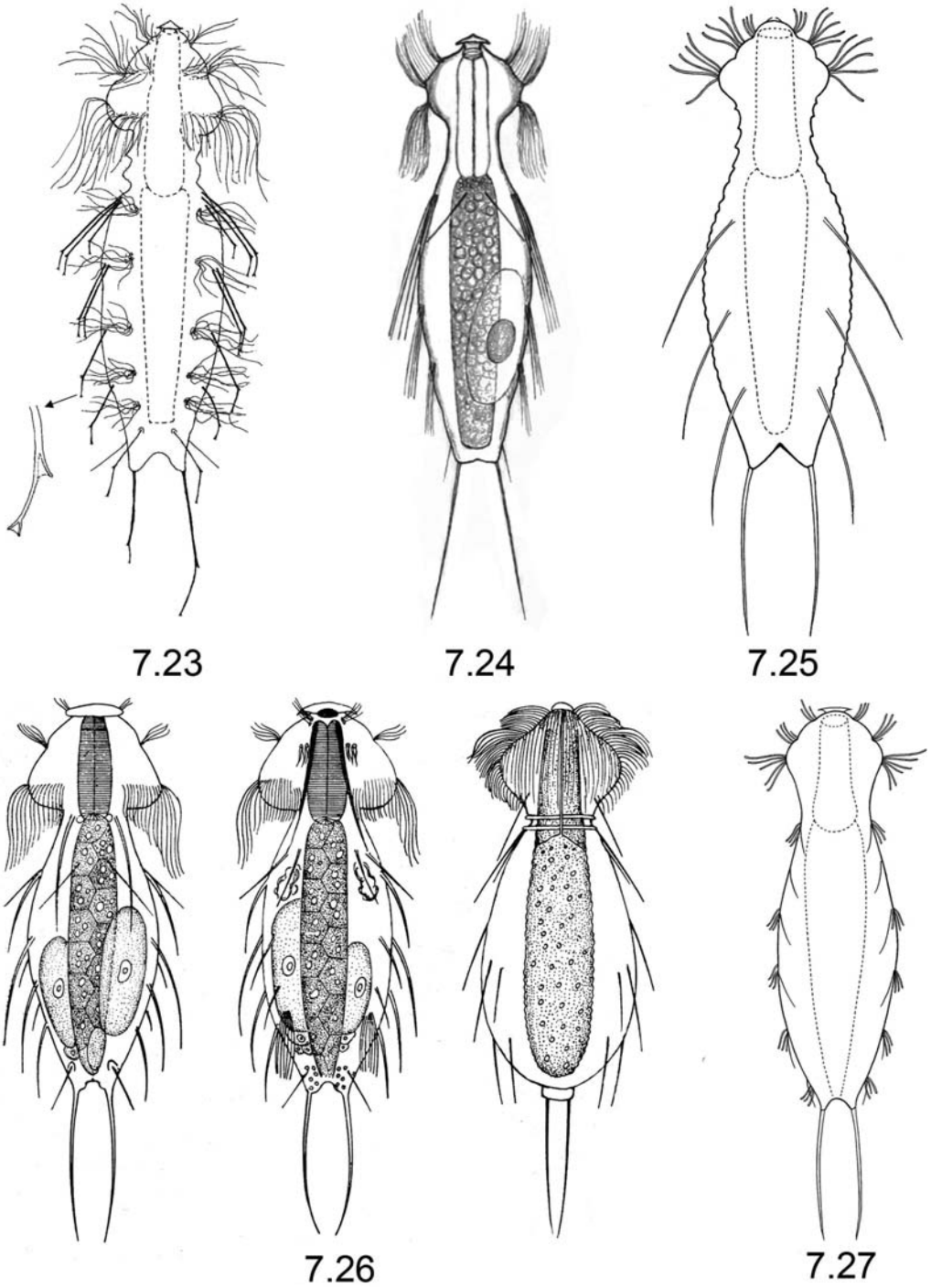


PLATE 7 Fig. 7.23 *Setopus chatticus* Schwank, 1990: ventral view with a detail of a ventrolateral spine (from Schwank, 1990 with permission); Fig. 7.24 *Setopus dubius* (Voigt, 1909): dorsal view (modified from Voigt, 1909); Fig. 7.25 *Setopus bisetosus* (Thompson, 1891): dorsal and ventral views (modified from Voigt, 1958), and dorsal view (modified from Thompson, 1891); Fig. 7.26 *Setopus primus* Grünspan, 1908: dorsal view (modified from Grünspan, 1908); Fig. 7.27 *Setopus iunctus* Greuter, 1917: dorsal view (modified from Greuter, 1917).

Gastrotricha: Chaetonotida: Dasydytidae: *Anacanthoderma:* Species

1 Only two long, caudal spines (Fig. 7.7) ..... *Anacanthoderma punctatum* Marcolongo, 1910
[Italy, Romania]

1′ Up to 16 long, spines distributed on the dorsolateral trunk (Fig. 7.8) ..... *Anacanthoderma paucisetosum* (Marcolongo, 1910)
[Italy, Romania]

Gastrotricha: Chaetonotida: Dasydytidae: *Haltidytes:* Species

1 A single paired group of lateral spines 2

1′ Two paired groups of lateral spines (Fig. 7.9) ..... *Haltidytes festinans* (Voigt, 1909)
[Germany, Poland, Romania, Russia, Ukraine]

2(1) Three paired ventral saltatorial spines (Fig. 7.10) ..... *Haltidytes crassus* (Greuter, 1917)
[Denmark, Italy, Romania, Russia, Sweden, Switzerland. Nearctic, Neotropics]

2′ One paired saltatorial spine (Fig. 7.11) ..... *Haltidytes saltitans* (Stokes, 1887)
[Italy, Germany, Romania, Russia]

Gastrotricha: Chaetonotida: Dasydytidae: *Chitonodytes:* Species

1 Three paired groups of double-barbed lateral spines, three paired cephalic ciliary tufts 2

1′ Single, simple lateral spines; uniform cephalic ciliature (Fig. 7.12) ..... *Chitonodytes longisetosus* (Metschikoff, 1865)
[Germany, Hungary, Italy, Romania, Switzerland]

2(1) Groups of 3-4-2 long lateral spines extending beyond the caudal end by up to half their length; cylindrical pharynx (Fig. 7.13) .....
..... *Chitonodytes longispinosus* (Greuter, 1917)
[Poland, Romania, Switzerland]

2′ Groups of 5-3-2 lateral spines extending beyond the caudal body end by up to ¼ of their length; bulbous pharynx (Fig. 7.14) .....
..... *Chitonodytes collini* (Remane, 1927)
[Germany, Romania]

Gastrotricha: Chaetonotida: Dasydytidae: *Stylochaeta:* Species

1 Short caudal styli; ventrolateral paired groups of long, spreadable spines on the trunk 2

1′ Long caudal styli, no spines on the trunk (Fig. 7.15) ..... *Stylochaeta stylifera* (Voigt, 1901)
[Germany, Hungary, Italy, Romania]

2(1) Three ventrolateral paired groups of double barbed spines; pharynx with posterior bulb 3

2′ Two ventrolateral paired groups of barbed spines; cylindrical pharynx (Fig. 7.16) ..... *Stylochaeta longispinosa* Greuter, 1917
[Germany, Poland, Romania, Switzerland]

3(2) Spines of the anteriormost group of decreasing length in a medial direction; two paired dorsolateral large plates followed by a short simple spine (Fig. 7.17) ..... *Stylochaeta scirtetica* Brunson, 1950
[Germany, Sweden]

3′ Spines of the anteriormost group of similar length; no dorsolateral plates or spines (Fig. 7.18) .. *Stylochaeta fusiformis* (Spencer, 1890)
[Widespread]

Gastrotricha: Chaetonotida: Dasydytidae: *Dasydytes*: Species

1 More than 50 lateral spines, with symmetrical arrangement; caudal spines long 2

1′ Less than 20 lateral spines, with clearly asymmetrical arrangement, 12 and 3 in number on each body side, respectively; caudal spines short (Fig. 7.19) ..... *Dasydytes* (*Dasydytes*) *asymmetricus* Schwank, 1990
[Germany]

2(1) Seven lateral paired spine groups/single spines; up to seven spines in each group; dorsally several small thin, barbed spines up to the caudal end (Fig. 7.20) ..... *Dasydytes* (*Dasydytes*) *goniathryx* Gosse, 1851
[Germany, Romania, Ukraine, United Kingdom]

2′ Eight lateral paired spine groups/single spines; up to five spines in each group; no dorsal spines (Fig. 7.21) ..... *Dasydytes* (*Dasydytes*) *ornatus* Voigt, 1909
[Bulgaria, France, Germany, Hungary, Italy, Poland, Romania, Switzerland, Ukraine, United Kingdom]

Gastrotricha: Chaetonotida: Dasydytidae: *Setopus*: Species

1 Caudal spines of inequal length; all spines barbed 2

1′ Caudal spines of equal length, all spines simple 3

2(1) Dorsal spines on head and neck; all spines barbed with a basal rudimental scale, ventral interciliary area scaled (Fig. 7.22) ..... *Setopus tongiorgii* (Balsamo, 1983)
[Italy, Poland, Sweden]

2′ No dorsal spines on head and neck; all spines double-barbed without basal rudimental scale; interciliary field smooth (Fig. 7.23) ..... *Setopus chatticus* Schwank, 1990
[Germany]

3(1) Lateral spines arranged into groups 4

3′ Lateral spines arranged singly 5

4(3) Three ventrolateral paired groups of 4-4-4 spines of the same length; no dorsal spines on the neck (Fig. 7.24) ..... *Setopus dubius* (Voigt, 1909)
[Germany, Hungary, Romania, Russia, Sweden]

4′ Four ventrolateral paired groups of 2-2-2-1 spines of different length; a paired dorsal spine on the neck (Fig. 7.25) ..... *Setopus bisetosus* (Thompson, 1891)
[Romania, Russia, United Kingdom].

5(3) Three paired lateral spines; cylindrical pharynx (Fig. 7.26) ..... *Setopus primus* Grünspan, 1908
[Hungary, Poland, Romania, Russia, Switzerland]

5′ Five paired lateral spines; pharynx with posterior bulb (Fig. 7.27) ..... *Setopus iunctus* Greuter, 1917
[Poland, Romania, Switzerland]

Gastrotricha: Chaetonotida: Dichaeturidae: *Dichaetura*: Species

1 Caudal paired appendages of very different length; dorsal cuticle smooth or finely scaled and spined 2

1′ Caudal paired appendages of the same length; dorsal cuticle with long, bent looped bristles arranged in columns (Fig. 7.28) ..... *Dichaetura piscator* (Murray, 1913)
[United Kingdom]

2(1) Caudal adhesive tubes bearing an inner well-developed curved process; a stout, dorsal intrafurcal spine 3

2′ Caudal adhesive tubes bearing an inner very short, straight accessory tube; dorsal cuticle smooth forming large transverse dorsolateral folds on the trunk; no intrafurcal spine (Fig. 7.29) ..... *Dichaetura capricornia* (Metschnikoff, 1865)
[Germany, France, Italy, Romania, Russia, Ukraine]

3(2) Caudal adhesive tubes bearing an inner well-developed curved hook (accessory tube?); dorsal cuticle covered with fine spined scales (Fig. 7.30) ..... *Dichaetura surreyi* Martin, 1990
[United Kingdom]

3′ Caudal adhesive tubes bearing an inner well-developed curved spine; dorsal cuticle smooth (Fig. 7.31) ..... *Dichaetura filispina* Suzuki & Furuya, 2013
[Japan]

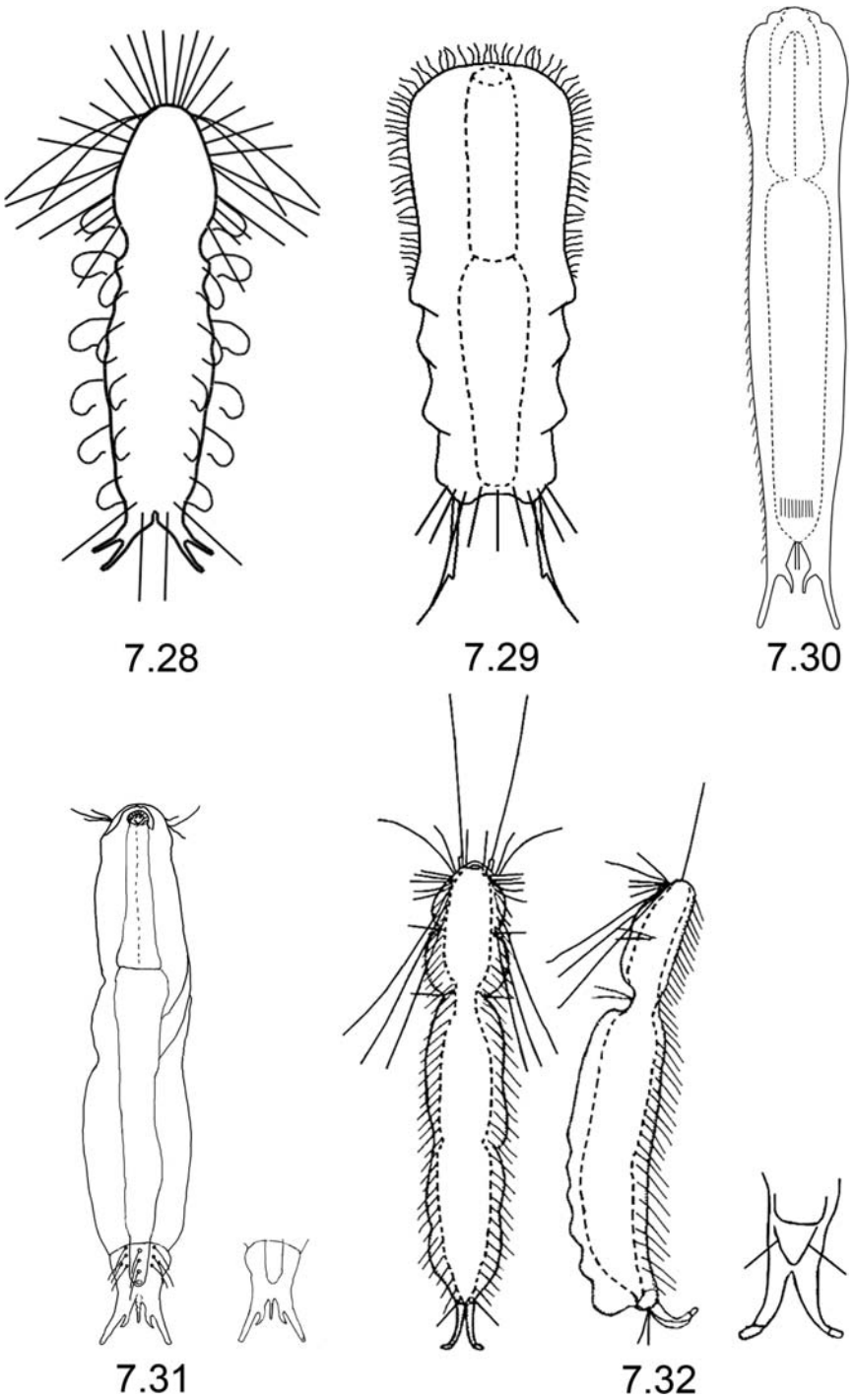


PLATE 8 Fig. 7.28 *Dichaetura piscator* (Murray, 1913): dorsal view (modified from Murray, 1913); Fig. 7.29 *Dichaetura capricornia* (Metschnikoff, 1865): dorsal view (from Balsamo, 1983 with permission); Fig. 7.30 *Dichaetura surreyi* Martin, 1990: dorsal view (spines are reported only on one side) (redrawn from Martin, 1990); Fig. 7.31 *Dichaetura filispina* Suzuki & Furuya, 2013: dorsal view and a detail of the ventral posterior end (modified from Suzuki et al., 2013); Fig. 7.32 *Proichtydioides remanei* Sudzuki, 1971: dorsal and ventral views with a detail of the posterior body end (modified from Sudzuki, 1971).

Gastrotricha: Chaetonotida: Chaetonotidae: Genera

This family also includes the recently described genus *Bifidochaetus*, which includes the new species *B. arcticus* and the species presented below as *Chaetonotus* (*Primochaetus*) *veronicae*; it is now *Bifidochaetus veronicae* (added in proof).

1 Furcal appendages shorter than 1/3 body length, unsegmented, with no scales or bristles; kephalion and epipleuria normal or small 2

1′ Furcal appendages usually very long (about 1/3 body length) and segmented, occasionally with very small scales and short bristles; kephalion and epipleuria large and protruding; common, epibenthic, periphytic, and interstitial (Figs. 7.33–39) ..... ***Polymerurus***

2(1) Body cuticle covered with smooth, keeled or spined scales 3

2′ Body cuticle smooth, occasionally thinly striped; rarely few spines at the furcal base; common, epibenthic, periphytic, and interstitial, also brackish water and marine (Figs. 7.40–59) ..... ***Ichthydium***

3(2) Smooth, stalked or keeled scales, generally numerous 4

3′ Numerous spined scales; spines short to very long, simple or barbed; very common, epibenthic, periphytic, and interstitial, also brackish water and marine (Figs. 7.60–186) ..... ***Chaetonotus***

4(3) Smooth, large, flat scales 5

4′ Stalked or keeled scales 7

5(4) Rounded or rhomboidal scales 6

5′ Polygonal scales; common, epibenthic, periphytic, and interstitial, rarely brackish water and marine (Figs. 7.187–197) ..... ***Lepidodermella***

6(5) Few to numerous rounded, spaced scales; very rare, periphytic (Figs. 7.198–200) ..... ***Fluxiderma***

6′ Numerous rhomboidal, juxtaposed scales; rare, periphytic (Fig. 7.201) ..... *Rhomballichtys punctatus* (Greuter, 1917)
[Italy, Poland, Romania, Russia, Switzerland]

7(4) Numerous stalked scales; common, epibenthic, periphytic, and interstitial, also brackish water and marine (Figs. 7.202–218) ..... ***Aspidiophorus***

7′ Numerous keeled scales; common, epibenthic, periphytic, and interstitial, also brackish water and marine (Figs. 7.219–236) ..... ***Heterolepidoderma***

Gastrotricha: Chaetonotida: Chaetonotidae: *Polymerurus*: Species

1 Furca long (1/3–1/5 body length) and thin, with long, usually segmented adhesive tubes 2

1′ Furca unusually short (1/10 body length), thick, unsegmented, with scale rudiments and strongly reduced adhesive tubes (Fig. 7.33) ..... *Polymerurus serraticaudus* (Voigt, 1901)
[Germany, Hungary, Italy, Poland, Romania, Russia]

2(1) No scales on the dorsal posterior trunk or on the adhesive tubes; segmented adhesive tubes 3

2′ Smooth, rectangular small scales on the dorsal posterior trunk and on the outer side of the adhesive tubes; unsegmented adhesive tubes (Fig. 7.34) ..... *Polymerurus squammofurcatus* (Preobrajenskaia, 1926)
[Hungary, Poland, Romania, Russia]

3(2) Body covered with smooth scales without spines 4

3′ Body covered with spined scales or spines 5

4(3) Cylindrical trunk; pedunculated dorsal scales (Fig. 7.35) ..... *Polymerurus rhomboides* (Stokes, 1887)
[Widespread]

4′ Trunk posteriorly swollen; unpedunculated dorsal scales (Fig. 7.36) ..... *Polymerurus longicaudatus* (Tatem, 1867)
[United Kingdom]

5(4) Body covered with spines of similar length 6

5′ Body covered with short spines; long spines on the furca base (Fig. 7.37) ..... *Polymerurus nodicaudus* (Voigt, 1901)
[Widespread]

6(5) Wide, rounded trunk; rhomboidal four keeled scales with long spines; dorsal caudal intrafurcal spines (Fig. 7.38) ..... *Polymerurus entzii* (Daday, 1882)
[Hungary, Romania]

6′ Cylindrical body; scales not visible, short spines; no caudal intrafurcal spines (Fig. 7.39) ..... *Polymerurus nodifurca* Marcolongo, 1910
[Italy, Romania]

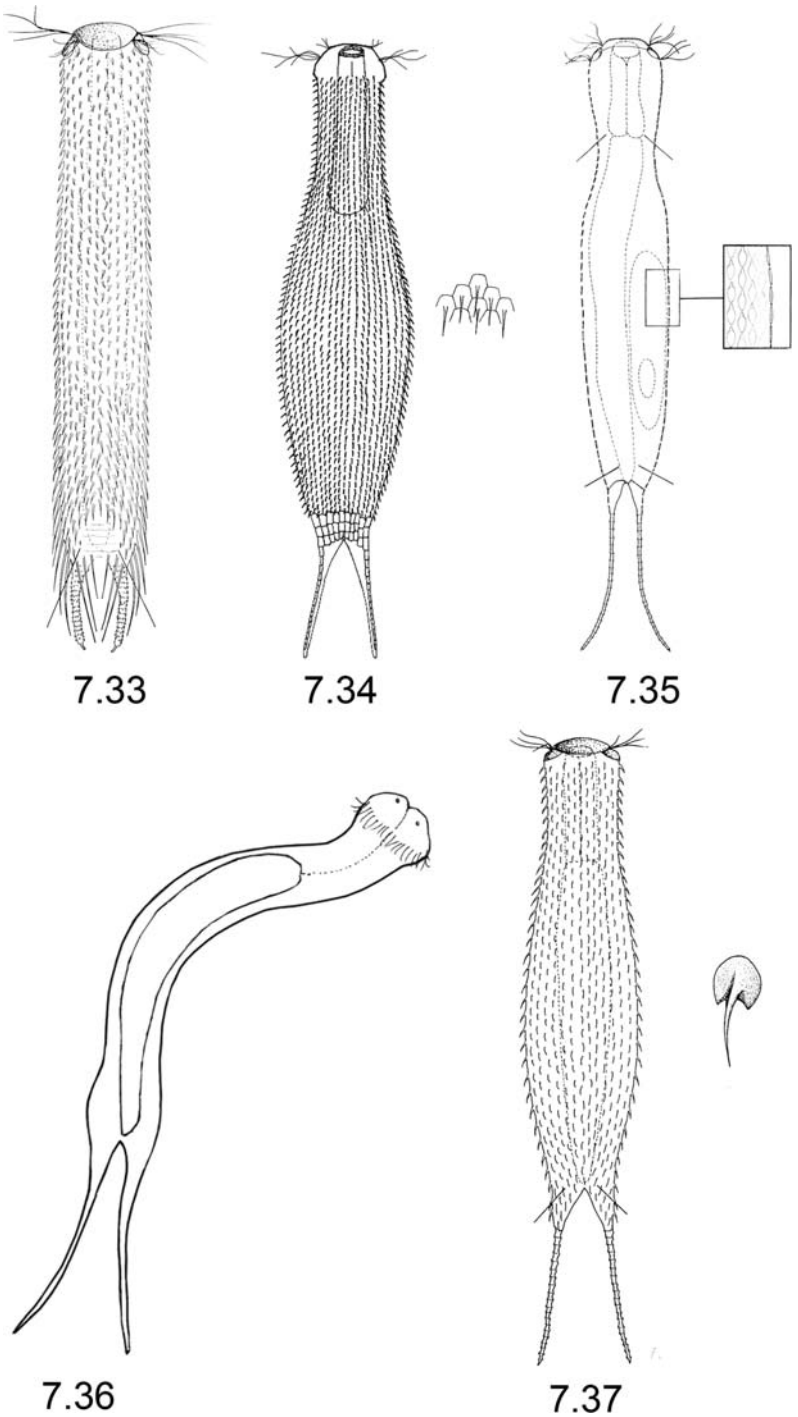
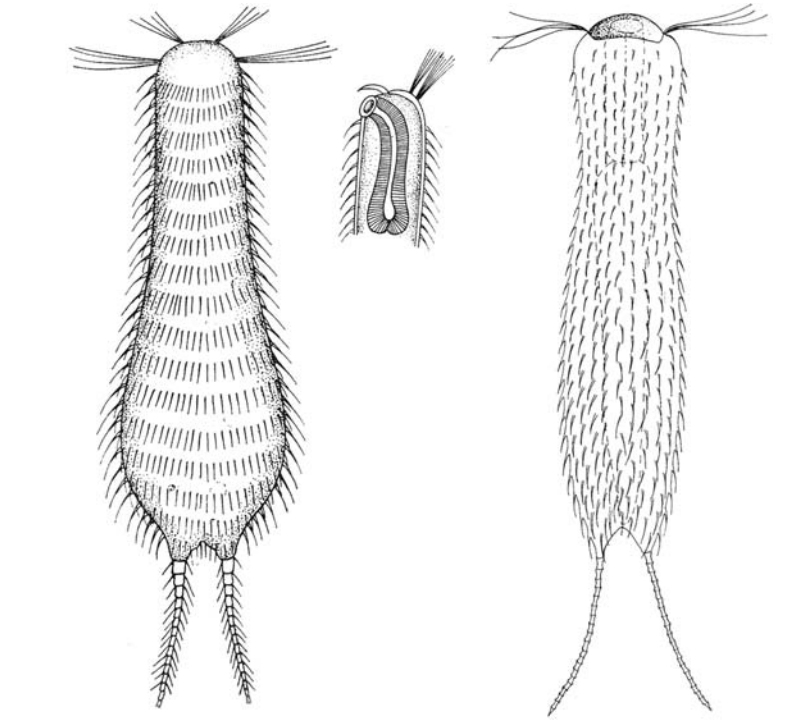


PLATE 9 Fig. 7.33 *Polymerurus serraticaudus* (Voigt, 1901): dorsal view (from Balsamo, 1983 with permission); Fig. 7.34 *Polymerurus squammofurcatus* (Preobrajenskaia, 1926): dorsal view with a detail of dorsal scales (modified from Preobrajenskaia, 1926); Fig. 7.35 *Polymerurus rhomboides* (Stokes, 1887): dorsal view with a detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.36 *Polymerurus longicaudatus* (Tatem, 1867): dorsal view (redrawn from Tatem, 1867); Fig. 7.37 *Polymerurus nodicaudus* (Voigt, 1901): dorsal view with a detail of a dorsal scale (from Balsamo, 1983 with permission).



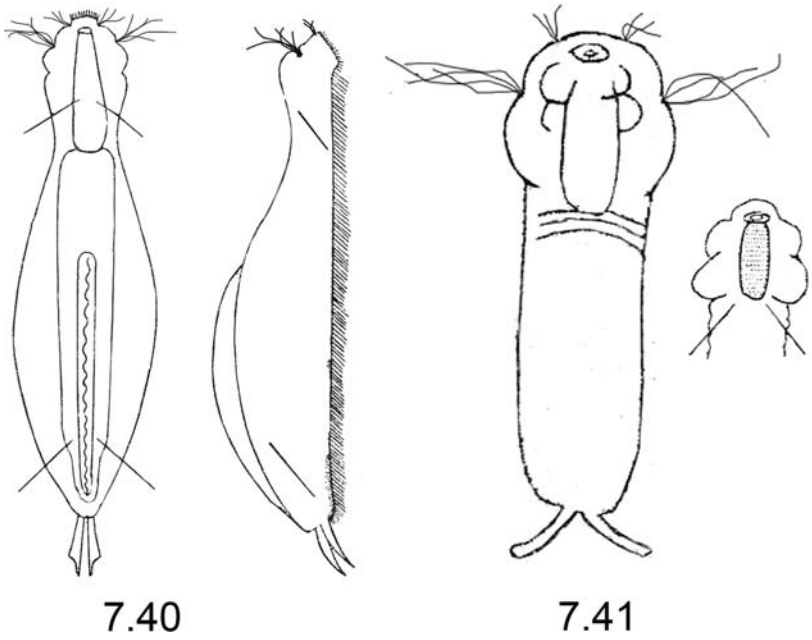


PLATE 10 Fig. 7.38 *Polymerurus entzii* (Daday, 1882): dorsal view, and lateral view of the head (modified from Rudescu, 1967); Fig. 7.39 *Polymerurus nodifurca* Marcolongo, 1910: dorsal view (from Balsamo, 1983 with permission); Fig. 7.40 *Ichthydium balatonicum* Rudescu, 1967: dorsal and lateral views (modified from Rudescu, 1967); Fig. 7.41 *Ichthydium macrocapitatum* Sudzuki, 1971: dorsal view with a detail of the dorsal head (modified from Sudzuki, 1971).

Gastrotricha: Chaetonotida: Chaetonotidae: *Ichthydium*: Species

1 Furca made of basal parts and adhesive tubes; no dorsal cuticular comb 2

1′ Furca made of the only adhesive tubes with concave tips prolonged medially; a longitudinal cuticular comb on the dorsal posterior trunk (Fig. 7.40) ..... *Ichthydium balatonicum* Rudescu, 1967
[Hungary, Romania]

2(1) Adhesive tubes very long (up to 3/4 furca length) 3

2′ Adhesive tubes normal or short 7

3(2) Adhesive tubes pincer-shaped; posterior cephalic lobes normally developed 4

3′ Adhesive tubes straight and diverging; posterior cephalic lobes strongly developed and protruding (Fig. 7.41) ..... *Ichthydium macrocapitatum* Sudzuki, 1971
[Japan]

4(3) Medium body size (>130 µm body length); posterior sensory bristles of normal length (<¼ body length) 5

4′ Small body size (<80 µm body length); posterior sensory bristles very long (1/4 body length) (Fig. 7.42) ..... *Ichthydium tanytrichum* Balsamo, 1983
[Italy, Sweden]

5(4) No dorsal or ventral scales 6

5′ Four paired keeled scales on the dorsal furca base; two ventral caudal keeled scales (Fig.7.43) ..... *Ichthydium skandicum* Kånneby et al., 2009
[Sweden]

6(5) Sensory bristles thickened; medial edge of the adhesive tubes with a bulge (Fig. 7.44) ..... *Ichthydium forcipatum* Voigt, 1902
[Widespread]

6′ Sensory bristles thin; medial edge of the adhesive tubes without a bulge (Fig. 7.45) ..... *Ichthydium forficula* Remane, 1927
[Bulgaria, Germany, Italy, Japan, Poland, Romania, Russia, United Kingdom]

7(2) Cuticle smooth with few scales or spines 8

7′ Cuticle smooth or very finely ornamented without scales or spines 11

8(7) Dorsal or ventral scales without spines 9

8′ Dorsal and/or ventral long spines without scales 10

9(8) A large transversal cuticular fold on the dorsal posterior trunk; no scales on the dorsal furca base; ventral field densely scaled (Fig. 7.46) ..... *Ichthydium plicatum* Balsamo & Fregni, 1995
[Italy]

9′ No dorsal cuticular fold; few scales on the dorsal furca base; two paired keeled scales on the ventral furca base (Fig. 7.47) ..... *Ichthydium squamigerum* Balsamo & Fregni, 1995
[Italy, Sweden]

10(8) One paired long, simple parafurcal spine (Fig. 7.48) ..... *Ichthydium diacanthum* Balsamo & Todaro, 1995
[Italy, Sweden]

10′ Two paired long simple spines, one dorsal and one ventral to the furca base (Fig. 7.49) ..... *Ichthydium dubium* Preobrajenskaia, 1926
[Romania; Russia]

11(7) Cuticle smooth 12

11′ Cuticle very finely ornamented 19

12(11) Dorsal cuticle without grooves 13

12′ Dorsal cuticle with 35–40 small transversal grooves well visible along the body edges; a bulge on the inner margin of the furca (Fig. 7.50) ..... *Ichthydium sulcatum* (Stokes, 1887)
[Germany, Poland, Romania]

13(12) Kephalion strongly developed; furca quite short (1/8–1/10 body length) 14

13′ Kephalion normal or small; furca normally developed 16

14(13) Kephalion extending beyond the head margin; no dorsal cuticular folds 15

14′ Kephalion rounded, not extending beyond the head margin; two large transversal cuticular folds on the dorsal posterior trunk (Fig. 7.51) ..... *Ichthydium rostrum* Roszczak, 1969
[Poland]

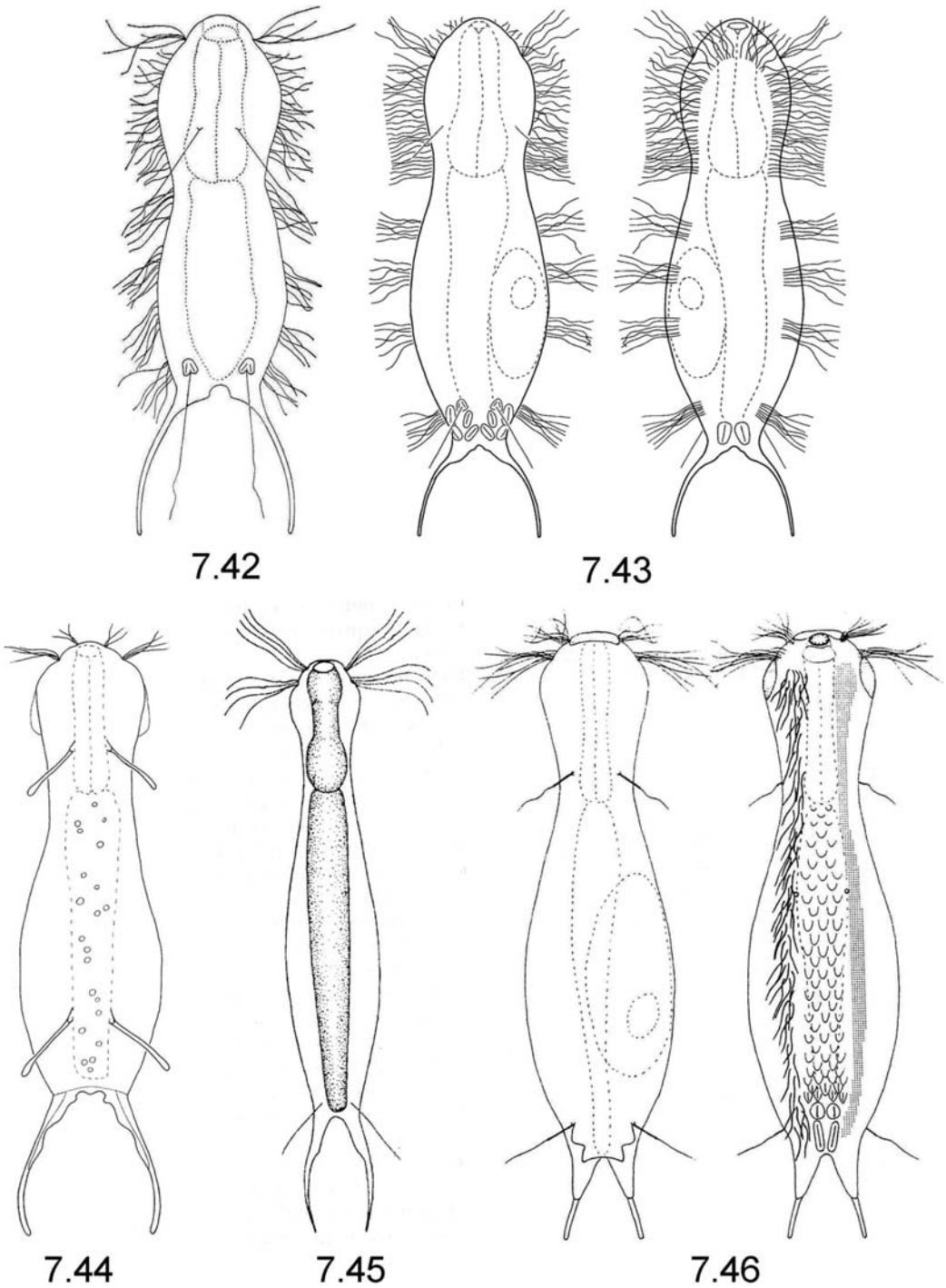


PLATE 11 Fig. 7.42 *Ichthydium tanytrichum* Balsamo, 1983: dorsal view (from Balsamo, 1983 with permission); Fig. 7.43 *Ichthydium skandicum* Kånneby, Todaro, & Jondelius, 2009: dorsal and ventral views (from Kånneby et al., 2009 with permission); Fig. 7.44 *Ichthydium forcipatum* Voigt, 1902: dorsal view (from Balsamo, 1983 with permission); Fig. 7.45 *Ichthydium forficula* Remane, 1927: dorsal view (modified from Remane, 1927); Fig. 7.46 *Ichthydium plicatum* Balsamo & Fregni, 1995: dorsal and ventral views (from Balsamo & Fregni, 1995 with permission).

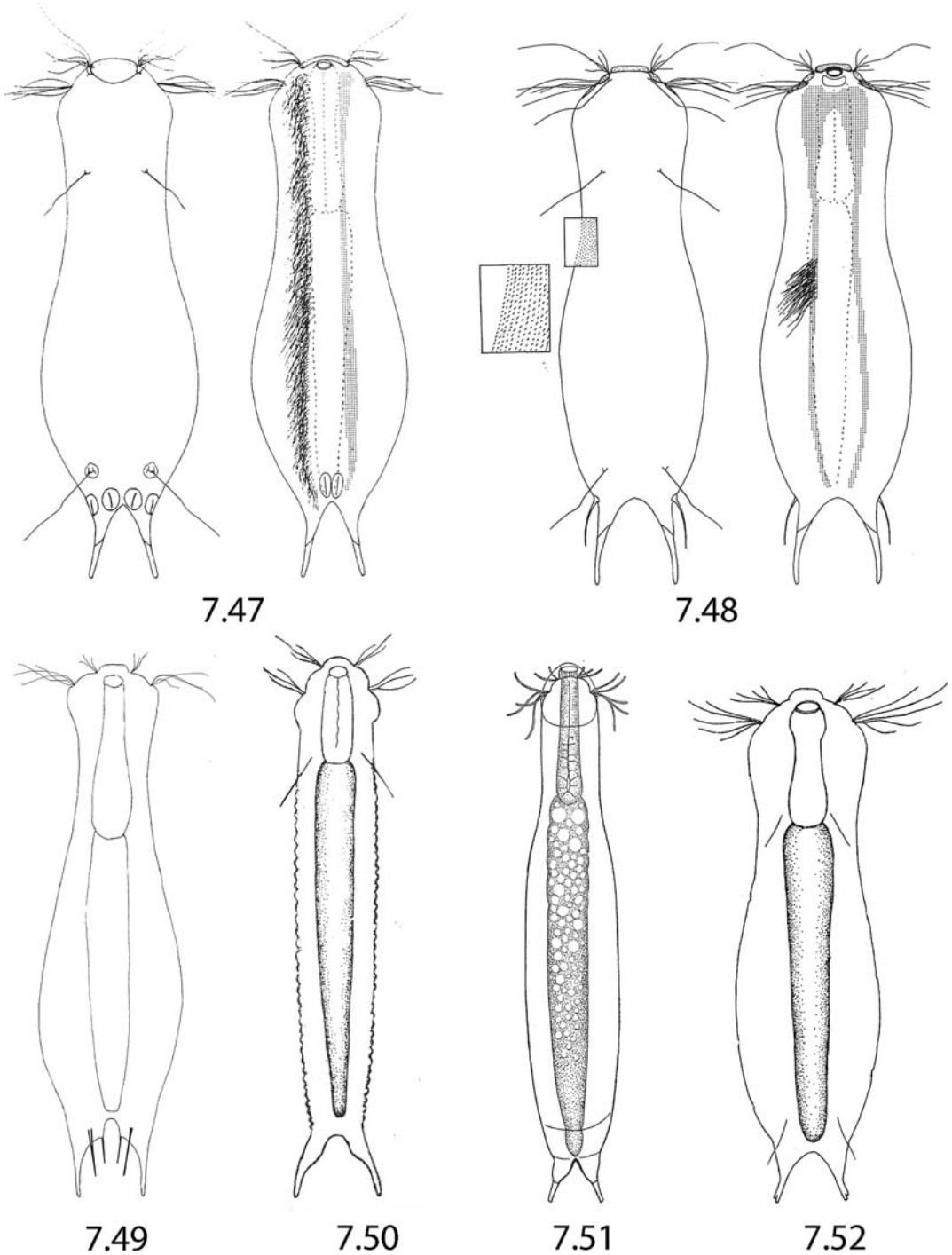


PLATE 12 Fig. 7.47 *Ichthydium squamigerum* Balsamo & Fregni, 1995: dorsal and ventral views (from Balsamo & Fregni, 1995 with permission); Fig. 7.48 *Ichthydium diacanthum* Balsamo & Todaro, 1995: dorsal and ventral views with a detail of the cuticular ornamentation (from Balsamo & Todaro, 1995 with permission); Fig. 7.49 *Ichthydium dubium* Preobrajenskaia, 1926: dorsal view; Fig. 7.50 *Ichthydium sulcatum* (Stokes, 1887): dorsal view; Fig. 7.51 *Ichthydium rostrum* Roszczak, 1969 (from Roszczak, 1969 with permission); Fig. 7.52 *Ichthydium bifurcatum* Preobrajenskaia, 1926: dorsal view ((from Kisielewski, 1998 with permission).

15(14) Kephalion hood-like extending anteriorly beyond the head margin; adhesive tubes with bifurcated tips (Fig. 7.52) ..... *Ichthydium bifurcatum* Preobrajenskaia, 1926
[Poland, Romania, Russia]

15′ Kephalion rectangular extending laterally beyond the head margin, normal adhesive tubes (Fig. 7.53) ..... *Ichthydium galeatum* Konsuloff, 1921
[Bulgaria, Romania]

16(13) Dorsal cuticle without folds; cephalic cilia of similar length 17

16′ Dorsal cuticle with several transversal folds; one paired very long cilium in the posterior cephalic ciliary tufts (Fig. 7.54) ..... *Ichthydium palustre* Kisielewski, 1981
[Poland]

17(16) Medium body size (130−190 µm); head wide as the trunk or narrower 18

17′ Large body size (>230 µm); head wider than the trunk (Fig. 7.55) ..... *Ichthydium maximum* Greuter, 1917
[Japan, Poland, Romania, Switzerland]

18(17) Trilobate, fusiform head with a paired evident ciliary tuft; intestine with a brownish anterior region (Fig. 7.56) ..... *Ichthydium bifasciale* Schwank, 1990
[Germany]

18′ Pentalobate head with two paired ciliary tufts; intestine uniform (Fig. 7.57) ..... *Ichthydium pellucidum* Preobrajenskaia, 1926
[Russia]

19(11) Fusiform, small-sized body (≤95 µm body length); cuticle with extremely fine longitudinal striations (Fig. 7.58) ..... *Ichthydium podura* (Müller, 1773)
[Russia]

19′ Elongate, medium-sized (120−140 µm body length); cuticle with 20−25 fine columns of 40−45 faint keeled elements (Fig. 7.59) ..... *Ichthydium fossae* d'Hondt, 1972
[France, Italy]

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus*: Subgenera

1 Uniform dorsal scale covering; one to several paired short to long parafurcal spines often present 2

1′ A dorsal transversal series of several long, thick, straight spines on the anterior trunk inserted on scales different from the others; a paired single, long to very long parafurcal spine (Figs. 7.60−67) ..... ***Chaetonotus* (*Zonochaeta*)**

2(1) Cuticle of normal thickness, not colored 3

2′ Very thick, three-layered cuticle, distinctly orange/brown in color, with an outer granular layer (Fig. 7.68) ..... *Chaetonotus (Tristratachaetus) rhombosquamatus* Kolicka, Kisielewski, Nesteruk & Zawierucha, 2013
[Poland]

3(2) Caudal adhesive tubes normally developed or very long; no intrafurcal hamulate spines 4

3′ Caudal adhesive tubes extremely reduced; one paired thick, short, hooked spine on the intrafurcal margin (Figs. 7.69−71) ..... ***Chaetonotus* (*Wolterecka*)**

4(2) Uniform body covering of spined scales similar in shape dorsally and ventrally; scales generally unkeeled 5

4′ Dorsal spined scales covering often not uniform and different from the ventral one; scales with 1−3 keels 6

5 (4) Rounded, flat scales with anterior double edge; thin, long, slightly bent dorsolateral spines caudally extending well beyond the furca; very long adhesive tubes (Figs. 7.72 and 73) ..... ***Chaetonotus* (*Lepidochaetus*)**

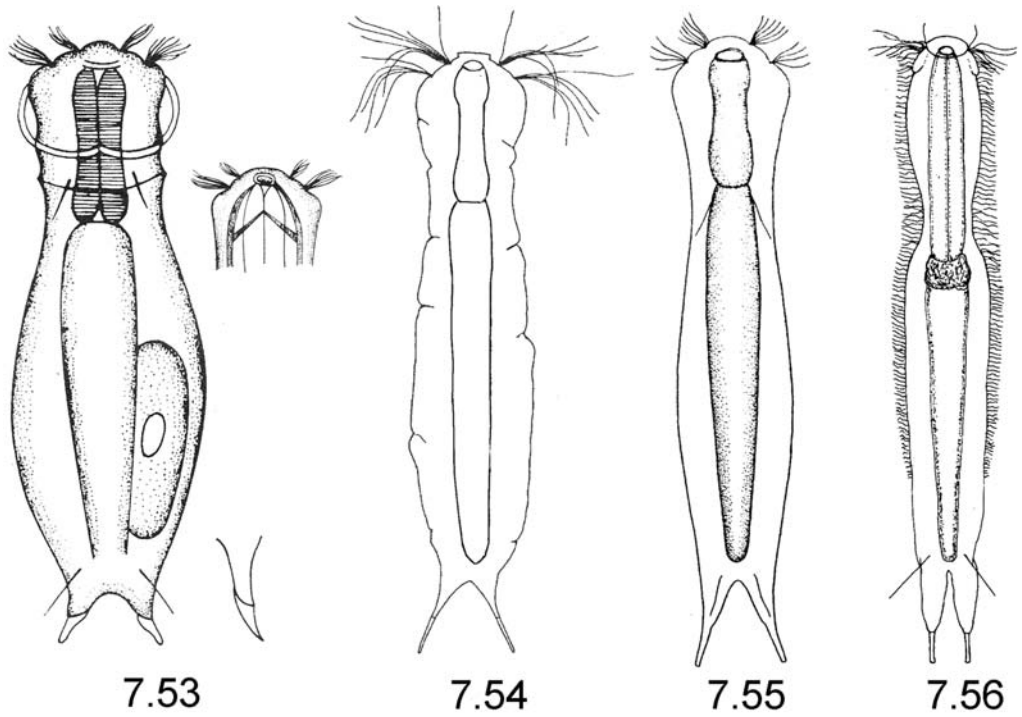
5′ Rounded or unilobed scales with single edge; thick, straight dorsolateral spines; generally 1−2 paired long parafurcal spine; medium-sized adhesive tubes (Figs. 7.74−95) ..... ***Chaetonotus* (*Primochaetus*)**

6(4) Dorsal spines simple or barbed, rarely double barbed, with accessory points inserted at different levels 7

6′ Dorsal spines double barbed with two accessory points inserted at the same level and occasionally an additional one more distal (Fig. 7.96) ..... *Chaetonotus* (*Schizochaetonotus*) *schultzei* Metschnikoff, 1865
[Widespread]

7(6) Hypostomion very large and strong with a transverse furrow; wide, extensible mouth ring with flattened units; large, cylindrical pharynx (Figs. 7.97−106) ..... ***Chaetonotus* (*Captochaetus*)**

7′ Hypostomion normally developed or reduced; mouth ring narrow to wide with rod-like units; narrow pharynx mostly with an anterior and a posterior thickenings (Figs. 7.107−187) ..... ***Chaetonotus* (*Chaetonotus*)**



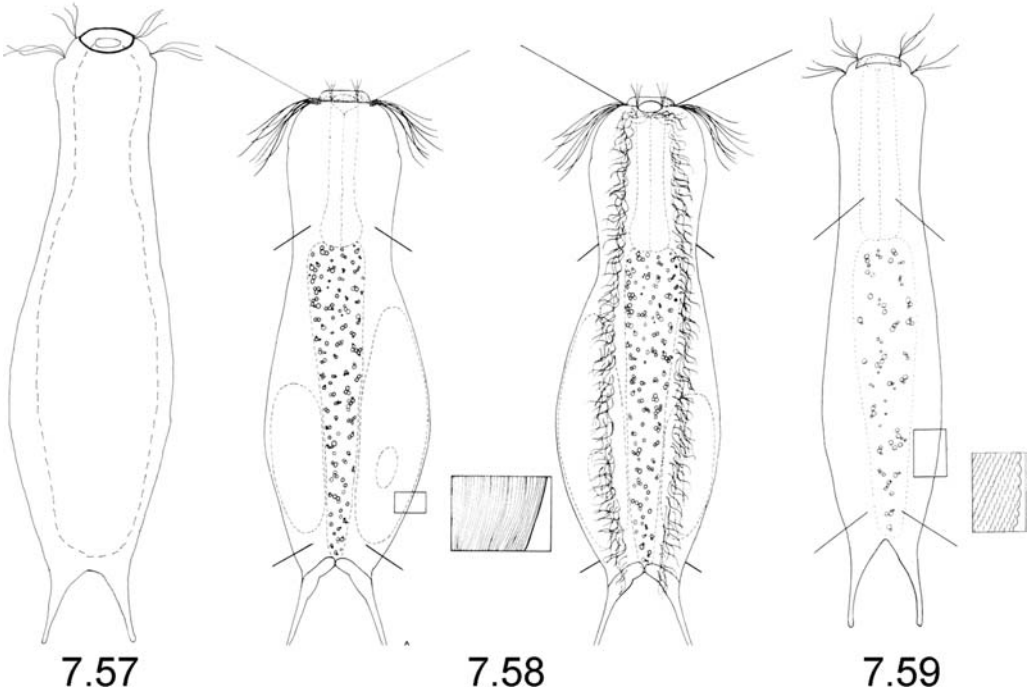


PLATE 13 Fig. 7.53 *Ichthydium galeatum* Konsuloff, 1921: dorsal view with details of the cephalic ventral ciliature and a caudal appendage (modified from Konsuloff, 1921); Fig. 7.54 *Ichthydium palustre* Kisielewski, 1981: dorsal view (redrawn from Kisielewski, 1981); Fig. 7.55 *Ichthydium maximum* Greuter, 1917: dorsal view (modified from Greuter, 1917); Fig. 7.56 *Ichthydium bifasciale* Schwank, 1990: dorsal view (from Schwank, 1990 with permission); Fig. 7.57 *Ichthydium pellucidum* Preobrajenskaia, 1926: dorsal view (modified from Preobrajenskaia 1926); Fig. 7.58 *Ichthydium podura* (Müller, 1773): dorsal and ventral views with a detail of the cuticular ornamentation (from Balsamo, 1983 with permission); Fig. 7.59 *Ichthydium fossae* d'Hondt, 1972: dorsal view with a detail of the cuticular ornamentation (from Balsamo, 1983 with permission).

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus (Zonochaeta)*: Species

1 Dorsal scales of similar shape; parafurcal spines shorter than or equal to furca 2

1′ Dorsal scales of various shape, parafurcal spines longer than furca 5

2(1) A dorsal series of 10−15 spines simple and straight; parafurcal simple spines slightly bent 3

2′ A dorsal series of five thick spines with concave apex; parafurcal spines and one unpaired dorsal median caudal spine thick, with concave apex (Fig. 7.60) ..... *Chaetonotus cestacanthus* Balsamo, 1990
[Italy]

3(2) A single dorsal series of spines; rounded to pentagonal scales with spiny process or short spine 4

3′ A dorsal series of 12 spines and an additional series of five spines on the posterior trunk; subtriangular scales with short spine (Fig. 7.61) ..... *Chaetonotus multisetosus* Preobrajenskaia, 1926
[Poland, Romania; Russia]

4(3) A dorsal series of 9−11 spines inserted on large, rounded scales; two paired parafurcal spines long $^{1}/_{2}$ to $^{2}/_{3}$ furca length (Fig. 7.62) ..... *Chaetonotus voigti* Greuter, 1917
[France, Germany, Romania, Switzerland, United Kingdom]

4′ A dorsal series of 13−15 spines with slightly enlarged base; two paired parafurcal spines shorter than $^{1}/_{2}$ furca length; a median long simple spine on the posterior trunk (Fig. 7.63) ..... *Chaetonotus caricicola* Schwank, 1990
[Germany]

5(1) A dorsal series of spines simple or with concave apex, long up to ¼ body length, inserted on the trunk; two paired parafurcal spines usually simple and quite spaced each from the other 6

5′ A dorsal series of spines barbed, extremely long (up to 2/3 body length), inserted on the neck base and extending beyond the furca; one paired parafurcal spine barbed, long twice the furca length (Fig. 7.64) ..... *Chaetonotus pentacanthus* Balsamo, 1981
[Italy]

6(5) A dorsal series of 7−20 thick, straight spines with concave apex, followed by 11 dorsal columns of elongate, hemi-elliptical keeled scales; ventral field with ∼11 columns of keeled scales 7

6′ A dorsal series of nine long, bent, simple spines, followed by seven dorsal columns of large keeled scales; ventral field with >20 columns of keeled scales (Fig. 7.65) ..... *Chaetonotus succinctus* Voigt, 1902
[Widespread]

7(6) A dorsal series of seven spines; posterior parafurcal spines barbed (Fig. 7.66) ..... *Chaetonotus dracunculus* Balsamo, 1990
[Italy]

7′ A dorsal series of 7−20 spines; posterior parafurcal spines simple (Fig. 7.67) ..... *Chaetonotus bisacer* Greuter, 1917
[Widespread]

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus* (*Wolterecka*): Species

1 Adhesive tubes unsegmented, not bifurcated; simple spines 2

1′ Adhesive tubes two segmented and with bifurcate tips; thick, barbed spines (Fig. 7.69) ..... *Chaetonotus dentatus* Tretjakova, 1992
[Russia]

2(1) Adhesive tubes extremely reduced (1/5 furca length), no marked narrowing of the posterior trunk (Fig. 7.70) ..... *Chaetonotus uncinus* Voigt, 1902
[Germany, Poland, Hungary, Romania, Italy, Russia]

2′ Adhesive tubes reduced (1/3 furca length), marked narrowing of posterior trunk (Fig. 7.71) ..... *Chaetonotus sudeticus* Kisielewski, 1984
[Poland]

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus* (*Lepidochaetus*): Species

1 Dorsal spines gradually increasing in length posteriorly; dorsal scales partially overlapping; dorsal caudal spines barbed (Fig. 7.72) ..... *Chaetonotus zelinkai* Grünspan, 1908
[Widespread]

1′ Dorsal spines on the posterior trunk much longer than the anterior ones; dorsal scales well-spaced; all spines simple (Fig. 7.73) ..... *Chaetonotus carpaticus* Rudescu, 1967
[Romania]

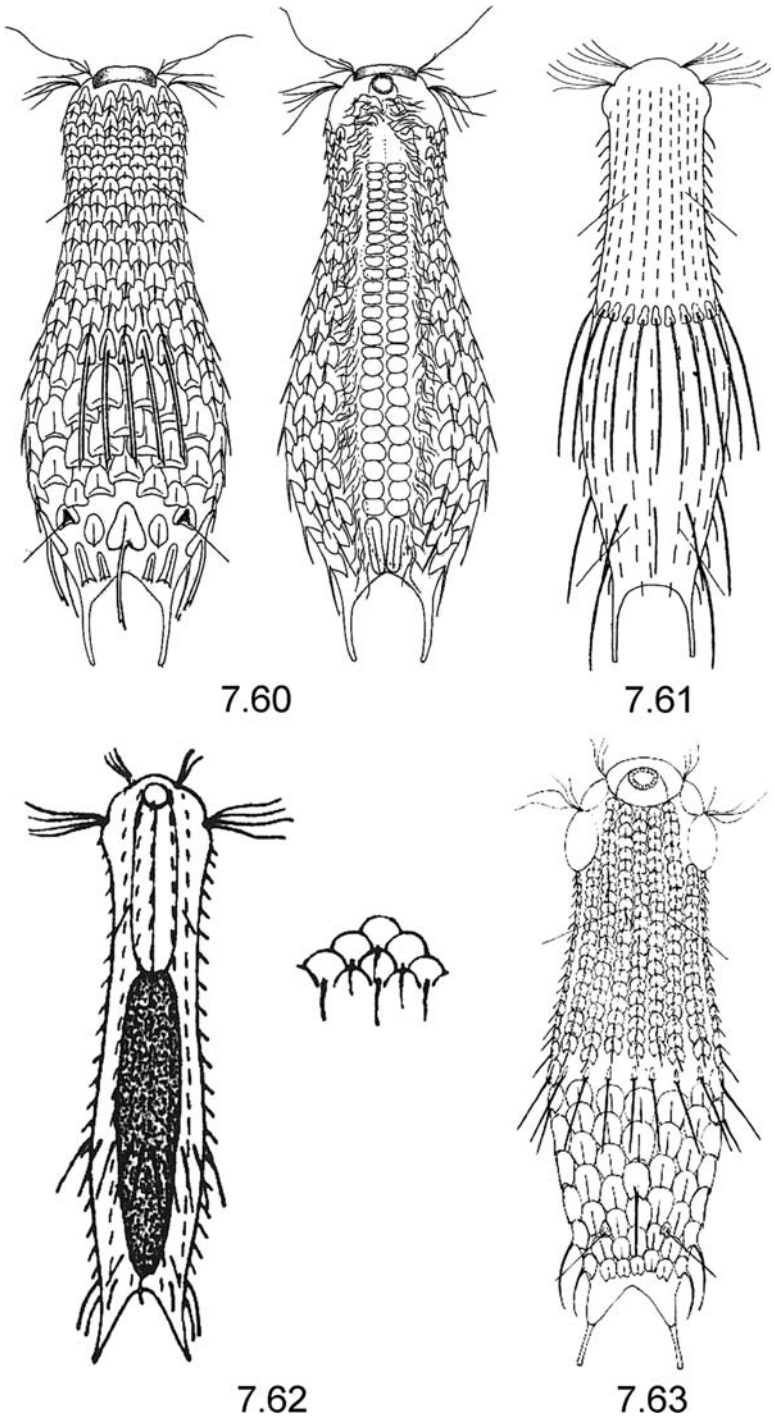
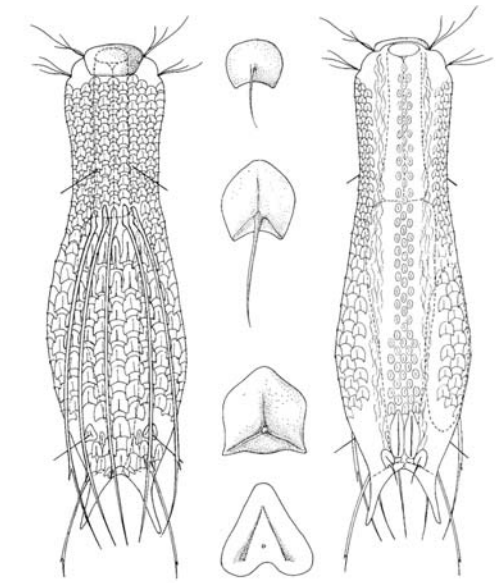
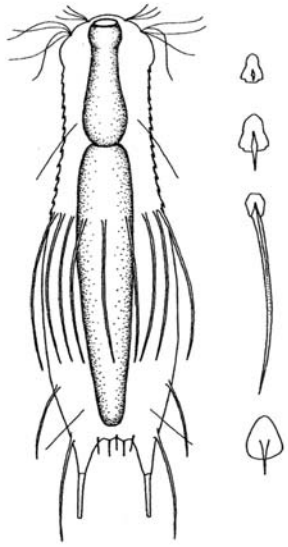


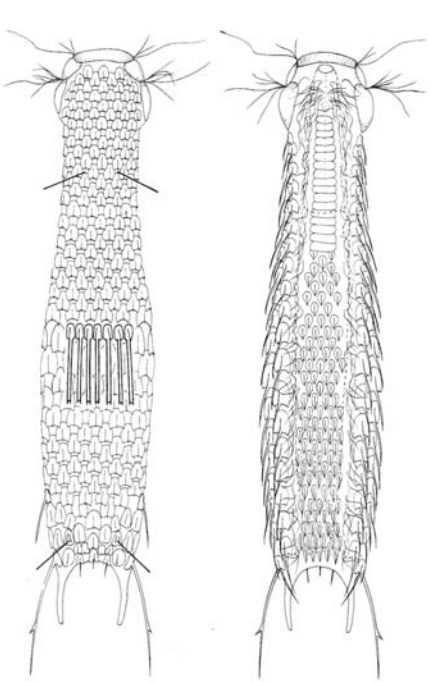
PLATE 14 Fig. 7.60 *Chaetonotus (Zonochaeta) cestacanthus* Balsamo, 1990: dorsal and ventral views (from Balsamo, 1990 with permission); Fig. 7.61 *Chaetonotus (Zonochaeta) multisetosus* Preobrajenskaia, 1926: dorsal view (from Kisielewski, 1998 with permission); Fig. 7.62 *Chaetonotus (Zonochaeta) voigti* Greuter, 1917: dorsal view with a detail of dorsal scales (modified from Greuter, 1917); Fig. 7.63 *Chaetonotus (Zonochaeta) caricicola* Schwank, 1990: dorsal view (redrawn from Schwank, 1990).



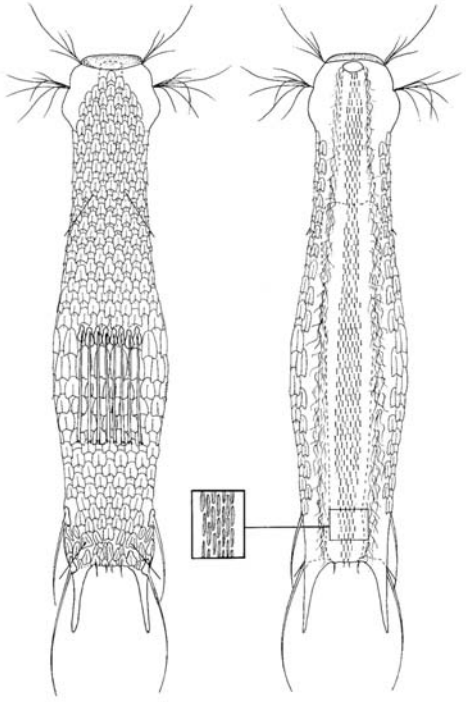
7.64



7.65



7.66



7.67

PLATE 15 Fig. 7.64 *Chaetonotus (Zonochaeta) pentacanthus* Balsamo, 1981: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.65 *Chaetonotus (Zonochaeta) succinctus* Voigt, 1902: dorsal view with details of dorsal scales (modified from Voigt, 1904); Fig. 7.66 *Chaetonotus (Zonochaeta) dracunculus* Balsamo, 1990: dorsal and ventral views (from Balsamo, 1990 with permission); Fig. 7.67 *Chaetonotus (Zonochaeta) bisacer* Greuter, 1917: dorsal and ventral views with a detail of ventral scales (from Balsamo, 1983 with permission).

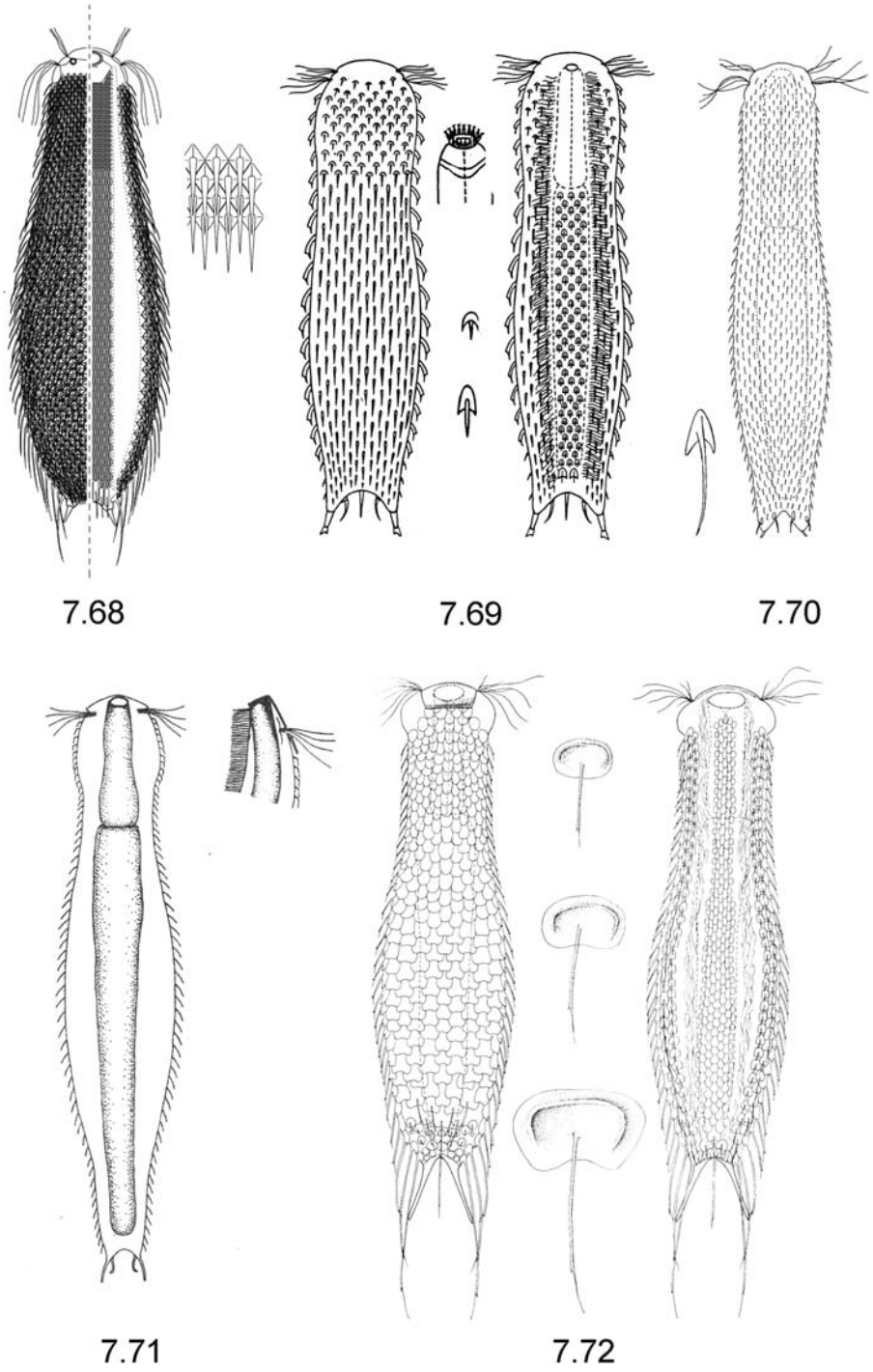


PLATE 16 Fig. 7.68 *Chaetonotus (Tristratachaetus) rhombosquamatus* Kolicka, Kisielewski, Nesteruk, & Zawierucha, 2013: schematic composition of dorsal view (*left*) and ventral view (*right*) with a detail of dorsal scales (modified from Kolicka et al. 2013); Fig. 7.69 *Chaetonotus (Wolterecka) dentatus* Tretjakova, 1992: dorsal and ventral views with details of the pharynx and dorsal scales (modified from Tretjakova, 1992); Fig. 7.70 *Chaetonotus (Wolterecka) uncinus* Voigt, 1902: dorsal view with details of a dorsal scale and the posterior body end (from Balsamo, 1983 with permission); Fig. 7.71 *Chaetonotus (Wolterecka) sudeticus* Kisielewski, 1984: dorsal view with a lateral view of the head (from Kisielewski, 1984 with permission); Fig. 7.72 *Chaetonotus (Lepidochaetus) zelinkai* Grünspan, 1908: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission).

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus* (*Primochaetus*): Species

1 Three to five lateral groups of 2−3 paired very long, thick, simple spines; dorsal spines thick, simple, and short, inserted on unkeeled scales 2

1′ Uniform covering of dorsal and lateral spines gradually increasing in length caudally; dorsal spines simple or barbed, scales unkeeled or keeled 5

2 (1) Three lateral groups of long spines; no intrafurcal spine; transversally elliptical scales 3

2′ Five lateral groups of very thick, long, straight spines; one unpaired long intrafurcal dorsal spine; pentagonal scales (Fig. 7.74) ..... *Chaetonotus rectaculeatus* Kisielewska, 1981
[Poland]

3(2) Dorsal scales small and spined 4

3′ Dorsal spined scales large and spined; some elongate keeled scales on the head (Fig. 7.75) ..... *Chaetonotus acanthocephalus* Valkanov, 1937
[Bulgaria, Germany, Poland]

4(3) Four long, thick simple dorsal spines on the head; long dorsal spines (Fig. 7.76) ..... *Chaetonotus striatus* Preobrajenskaia, 1926
[Romania, Russia]

4′ No long, thick dorsal spine on the head; short dorsal spines (Fig. 7.77) ..... *Chaetonotus bogdanovii* (Schimkewitsch, 1886)
[Russia]

5(1) Dorsal spines increasing in length up to mid trunk; dorsal posterior trunk bare or with smooth scales or short spines 6

5′ Dorsal spines increasing in length up to the caudal body end; dorsal posterior trunk with spined scales 14

6(5) Dorsal posterior trunk with scales or spines 7

6′ Dorsal posterior trunk bare; very small, square dorsal scales; one paired parafurcal simple spine much longer than the furca (Fig. 7.78) ..... *Chaetonotus arquatus* Voigt, 1903
[Germany, Hungary, Poland, Romania]

7(6) Very elongate body with caudal-most trunk region clearly distinct, long and narrower 8

7′ Fusiform body 11

8(7) Very long furca with long pointed adhesive tubes (up to 4/5 furca length); dorsal posterior scales with a keel or spiny process; two paired long parafurcal spines 9

8′ Normal or short furca; dorsal posterior scales smooth; 1−2 paired short parafurcal spines 10

9(8) Parafurcal spines close each other on each body side; two paired dorsal intrafurcal spines; small round ventral scales; cylindrical pharynx (Fig. 7.79) ..... *Chaetonotus heteracanthus* Remane, 1927
[Germany, Poland, Romania, Sweden, United Kingdom]

9′ Parafurcal spines spaced out on each body side; no intrafurcal spine; 11 or 12 rectangular ventral plates; pharynx with two marked bulbs at the extremities (Fig. 7.80) ..... *Chaetonotus soberanus* Grosso & Drahg, 1983
[Sweden. Neotropics]

10(8) Last lateral trunk spine three times as long than previous ones; one paired parafurcal spine (Fig. 7.81) ..... *Chaetonotus tenuis* Grünspan, 1908
[Austria, Germany, Poland, Romania, Russia]

10′ Last lateral spine only slightly longer than previous ones; two paired parafurcal spines (Fig. 7.82) ..... *Chaetonotus vechovi* Tretjakova, 1992
[Russia]

11(7) Adhesive tubes normally developed; dorsal scales rounded, posteriorly concave without keel 12

11′ Adhesive tubes absent, furca base short and broad with small scales and four paired long simple spines; dorsal scales pentagonal with two transversal keels (Fig. 7.83) ..... *Chaetonotus brachyurus* Balsamo, 1981
[Italy]

12(11) Less than ten dorsal columns of small scales; posterior trunk covered with smooth scales 13

12′ Four dorsal columns of large scales; posterior trunk with few small spined scales (Fig. 7.84) ..... *Chaetonotus macrolepidotus* Greuter, 1917
[Poland, Romania, Russia, Switzerland]

13(12) Dorsal longest spines arranged in a series of 7−12; furca base scaled (Fig. 7.85) ..... *Chaetonotus acanthodes* Stokes, 1887
[Poland, Romania, Russia, Sweden]

13′ Dorsal longest spines arranged in a series of five; furca base bare (Fig. 7.86) ..... *Chaetonotus ploenensis* Voigt, 1909
[Germany, Romania, Russia]

14(5) Simple, thin spines 15

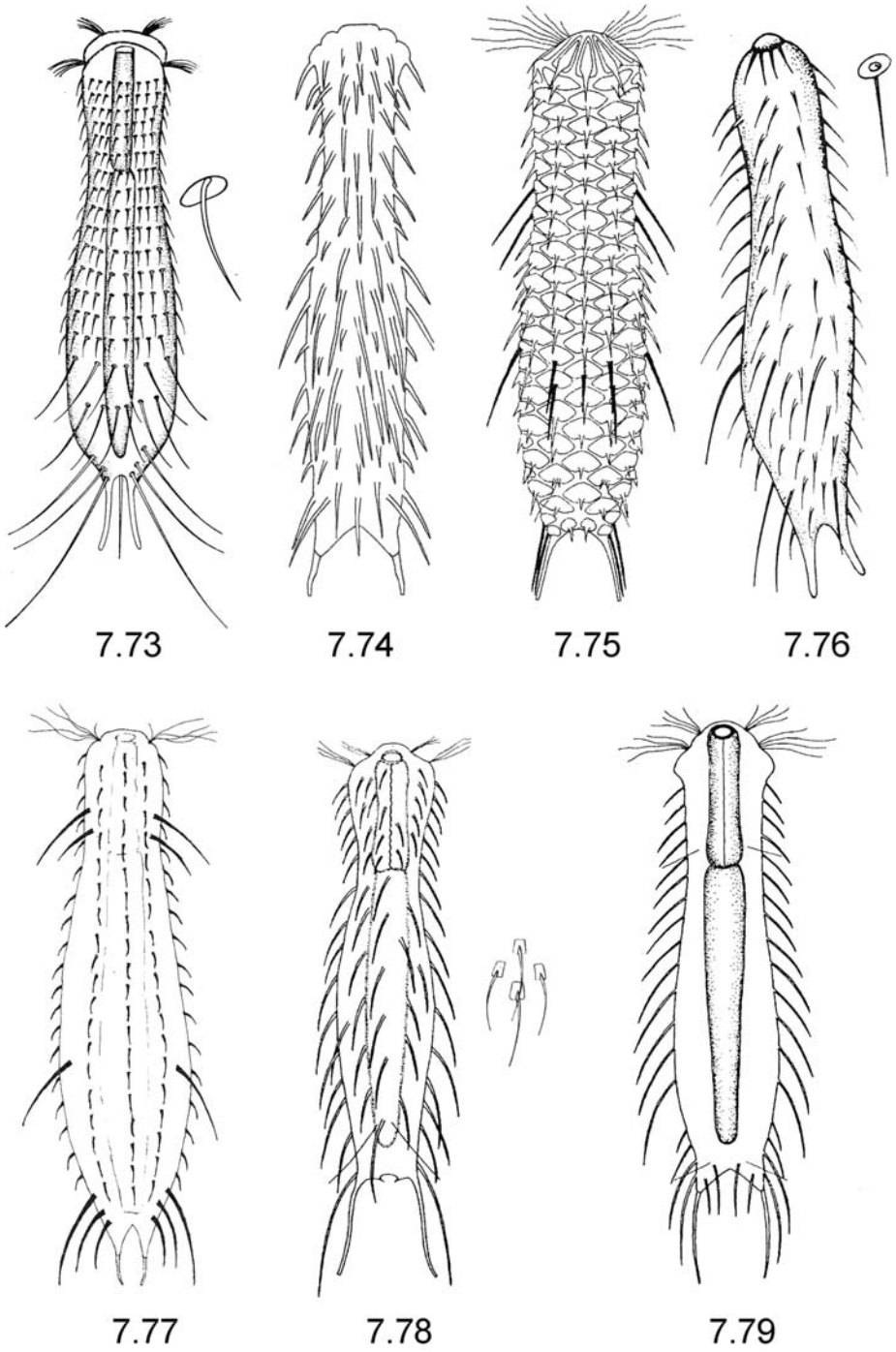


PLATE 17 Fig. 7.73 *Chaetonotus (Lepidochaetus) carpaticus* Rudescu, 1967: dorsal view with a detail of a dorsal scale (modified from Rudescu, 1967); Fig. 7.74 *Chaetonotus (Primochaetus) rectaculeatus* Kisielewska, 1981: dorsal view (from Kisielewska, 1981 with permission); Fig. 7.75 *Chaetonotus (Primochaetus) acanthocephalus* Valkanov, 1937: dorsal view (modified from Valkanov, 1937); Fig. 7.76 *Chaetonotus (Primochaetus) striatus* Preobrajenskaia, 1926: dorsal view with a detail of a dorsal scale (modified from Preobrajenskaia, 1926); Fig. 7.77 *Chaetonotus (Primochaetus) bogdanovii* (Schimkewitsch, 1886): dorsal view (modified from Schimkewitsch, 1886); Fig. 7.78 *Chaetonotus (Primochaetus) arquatus* Voigt, 1903: dorsal view with a detail of dorsal scales (modified from Voigt, 1903); Fig. 7.79 *Chaetonotus (Primochaetus) heteracanthus* Remane, 1927: dorsal view ((modified from Remane, 1927).

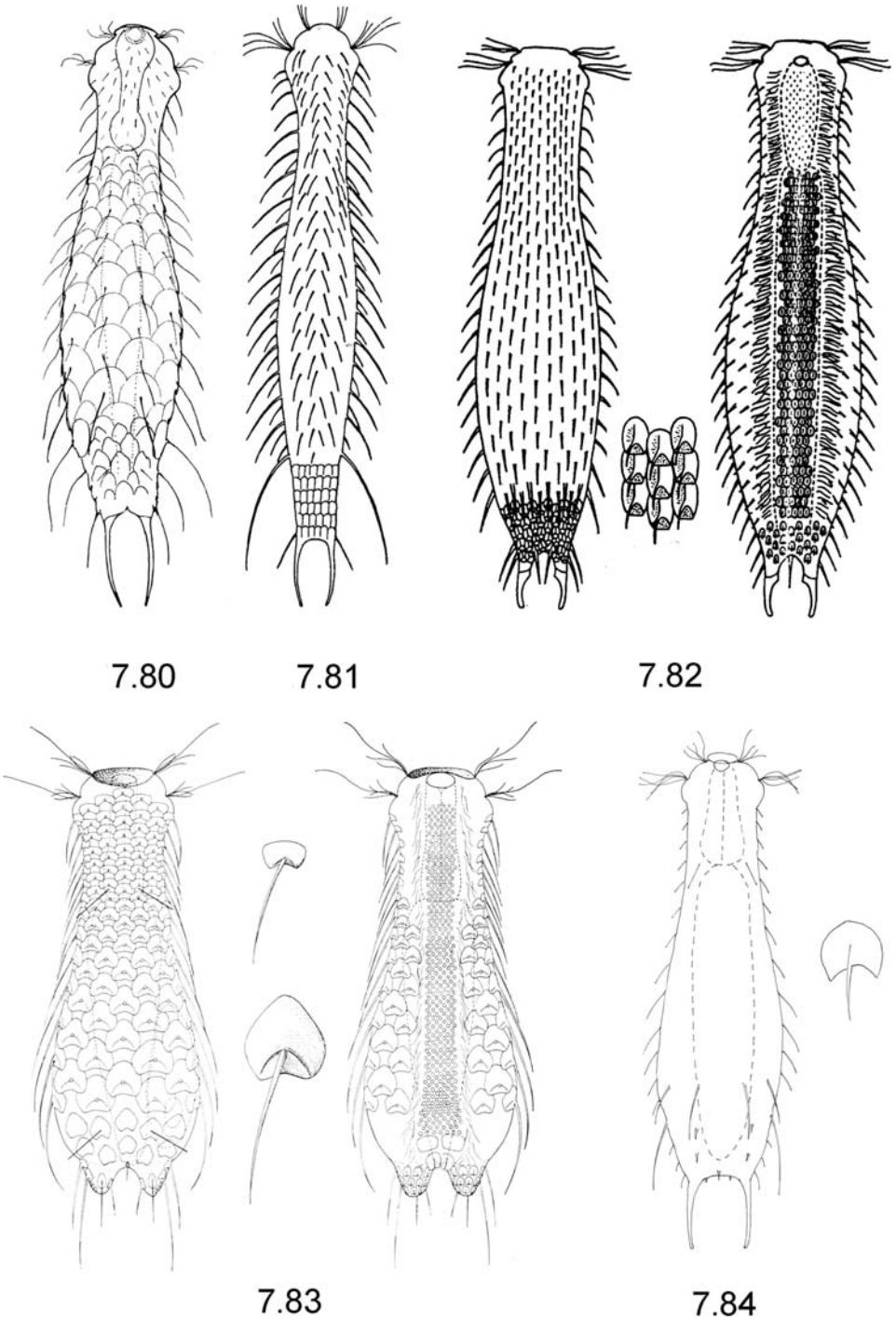


PLATE 18 Fig. 7.80 *Chaetonotus (Primochaetus) soberanus* Grosso & Drahg, 1983: dorsal view (modified from Grosso & Drahg, 1983); Fig. 7.81 *Chaetonotus (Primochaetus) tenuis* Grünspan, 1908: dorsal view (modified from Grünspan, 1908); Fig. 7.82 *Chaetonotus (Primochaetus) vechovi* Tretjakova, 1992: dorsal and ventral views with details of dorsal scales (modified from Tretjakova, 1992); Fig. 7.83 *Chaetonotus (Primochaetus) brachyurus* Balsamo, 1981: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.84 *Chaetonotus (Primochaetus) macrolepidotus* Greuter, 1917: dorsal view with detail of a dorsal scale (modified from Greuter, 1917).

14′ Barbed, thick spines 18

15(14) Rounded to suboval scales; head not elongate 16

15′ Hexagonal, small scales; very elongate head; three paired long, thick dorsal caudal spines (Fig. 7.87) ..... *Chaetonotus scoticus* Schwank, 1990
[Germany]

16(15) Small scales; ≥11 dorsal columns of scales; cylindrical pharynx 17

16′ Large scales with two keels; seven dorsal columns of 22–27 scales; pharynx with a marked posterior bulb (Fig. 7.88) ..... *Chaetonotus rotundus* Greuter, 1917
[Germany, Poland, Switzerland]

17(16) Scales with three keels; dorsal spines slightly bent; 11–13 dorsal columns of 22–23 scales (Fig. 7.89) ..... *Chaetonotus mutinensis* Balsamo, 1978
[Germany, Italy, Sweden]

17′ Scales with no keel; dorsal spines strongly bent; 16–19 dorsal columns of 27–30 scales (Fig. 7.90) ..... *Chaetonotus veronicae* Kånneby, 2013
[Sweden]

This species is now *Bifidochaetus veronicae* (Kanneby, 2013)

18(14) Parafurcal spines shorter than furca or absent 19

18′ Parafurcal spines longer than furca 21

19(18) Two to three paired parafurcal spines; no intrafurcal spine; large transversally elliptical scales 20

19′ Parafurcal spines absent; one paired thick dorsal intrafurcal spine; elongate elliptical scales (Fig. 7.91) ..... *Chaetonotus chuni* Voigt, 1901
[Widespread]

20(19) Two paired parafurcal spines of different length; scales spaced (Fig. 7.92) ..... *Chaetonotus armatus* Kisielewski, 1981
[Poland, Russia, Sweden]

20′ Three paired parafurcal spines of the same length; scales overlapping (Fig. 7.93) ..... *Chaetonotus scutulatus* Martin, 1981
[United Kingdom]

21(18) Barbed spines clearly bent at the insertion of the accessory point; two paired parafurcal spines; 1–2 paired dorsal intrafurcal spines shorter than furca (Fig. 7.94) ..... *Chaetonotus heideri* Brehm, 1917
[Widespread]

21′ Barbed spines straight or scarcely bent; three paired parafurcal spines; three unpaired dorsal intrafurcal spines all much longer than furca (Fig. 7.95) ..... *Chaetonotus cordiformis* Greuter, 1917
[Japan, Poland, Romania, Switzerland]

Gastrotricha: Chaetonotida: Chaetonotidae: Chaetonotus (*Captochaetus*): Species

1 Large or medium body size (<500 µm); dorsal scales not mitre-form and with simple spines 2

1′ Very large body size (>500 µm); dorsal peculiar subtriangular mitre-form scales with transversal striations and barbed spines (Fig. 7.97) ..... *Chaetonotus robustus* Davison, 1938
[Poland]

2(1) Dorsal scales pentagonal or subtriangular; dorsal caudal trunk covered with spines or scales 3

2′ Dorsal scales rounded posteriorly concave; dorsal caudal trunk covered with very short spines (Fig. 7.98) ..... *Chaetonotus insigniformis* Greuter, 1917
[Poland, Russia, Switzerland]

3(2) Dorsal scales pentagonal or subtriangular with relatively long spines; no cuticular folds 4

3′ Dorsal scales hastate with very fine, short simple spines; flexible body cuticle forming folds during locomotion (Fig. 7.99) ..... *Chaetonotus segnis* Martin, 1981
[United Kingdom]

4(3) Pentagonal scales. 5

4′ Subtriangular scales. 6

5(4) Furca base bare; scales with equal sides (Fig. 7.100) ..... *Chaetonotus simrothi* Voigt, 1909
[Germany, Hungary, Italy, Japan, Poland, Romania]

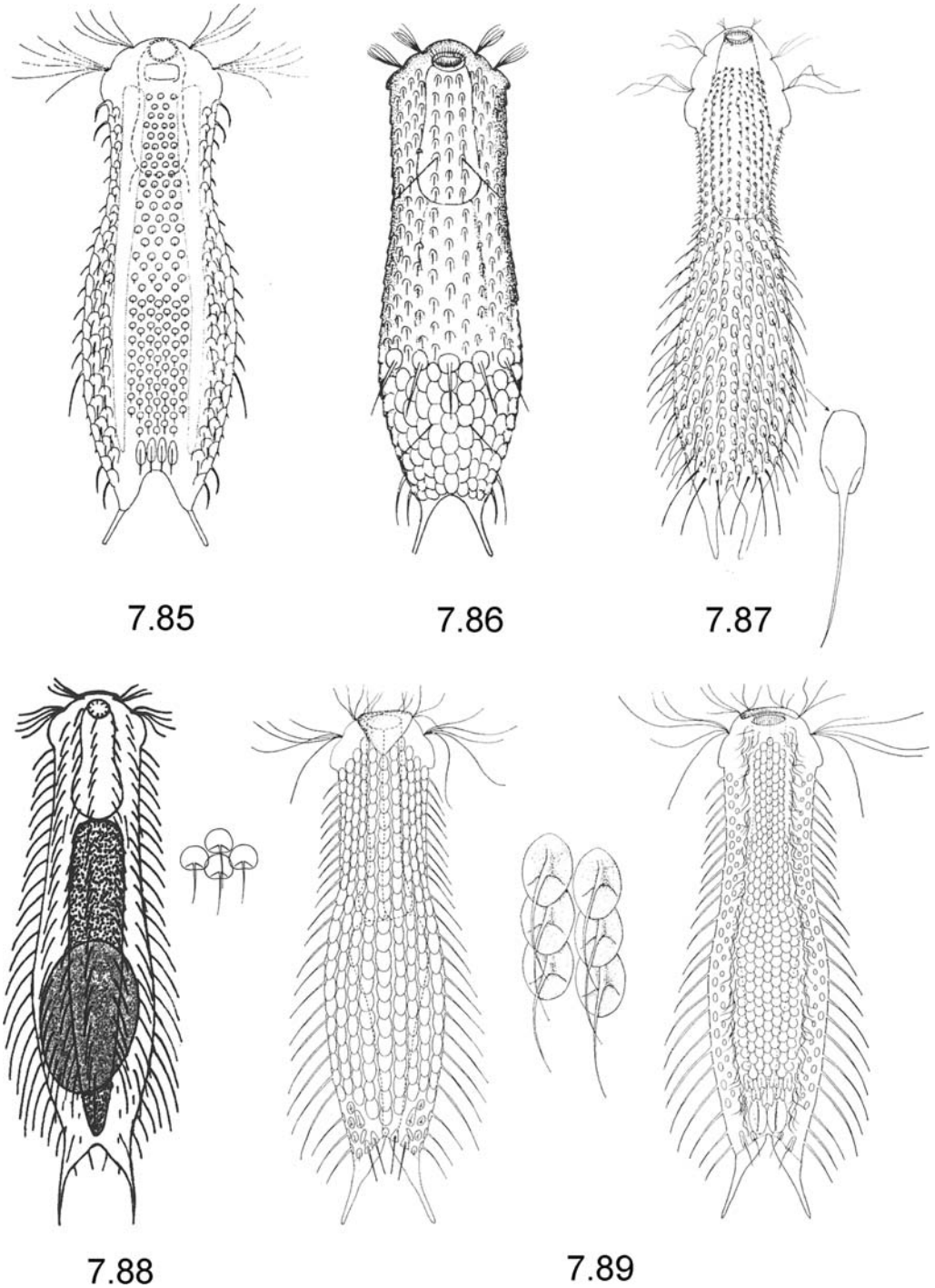


PLATE 19 Fig. 7.85 *Chaetonotus (Primochaetus) acanthodes* Stokes, 1887: ventral view (modified from Stokes, 1887); Fig. 7.86 *Chaetonotus (Primochaetus) ploenensis* Voigt, 1909: dorsal view (modified from Rudescu, 1967); Fig. 7.87 *Chaetonotus (Primochaetus) scoticus* Schwank, 1990: dorsal view with detail of a dorsal scale (redrawn from Schwank, 1990); Fig. 7.88 *Chaetonotus (Primochaetus) rotundus* Greuter, 1917: dorsal view with details of dorsal scales (modified from Greuter, 1917); Fig. 7.89 *Chaetonotus (Primochaetus) mutinensis* Balsamo, 1978: dorsal and ventral views with detail of dorsal scales (from Balsamo, 1983 with permission).

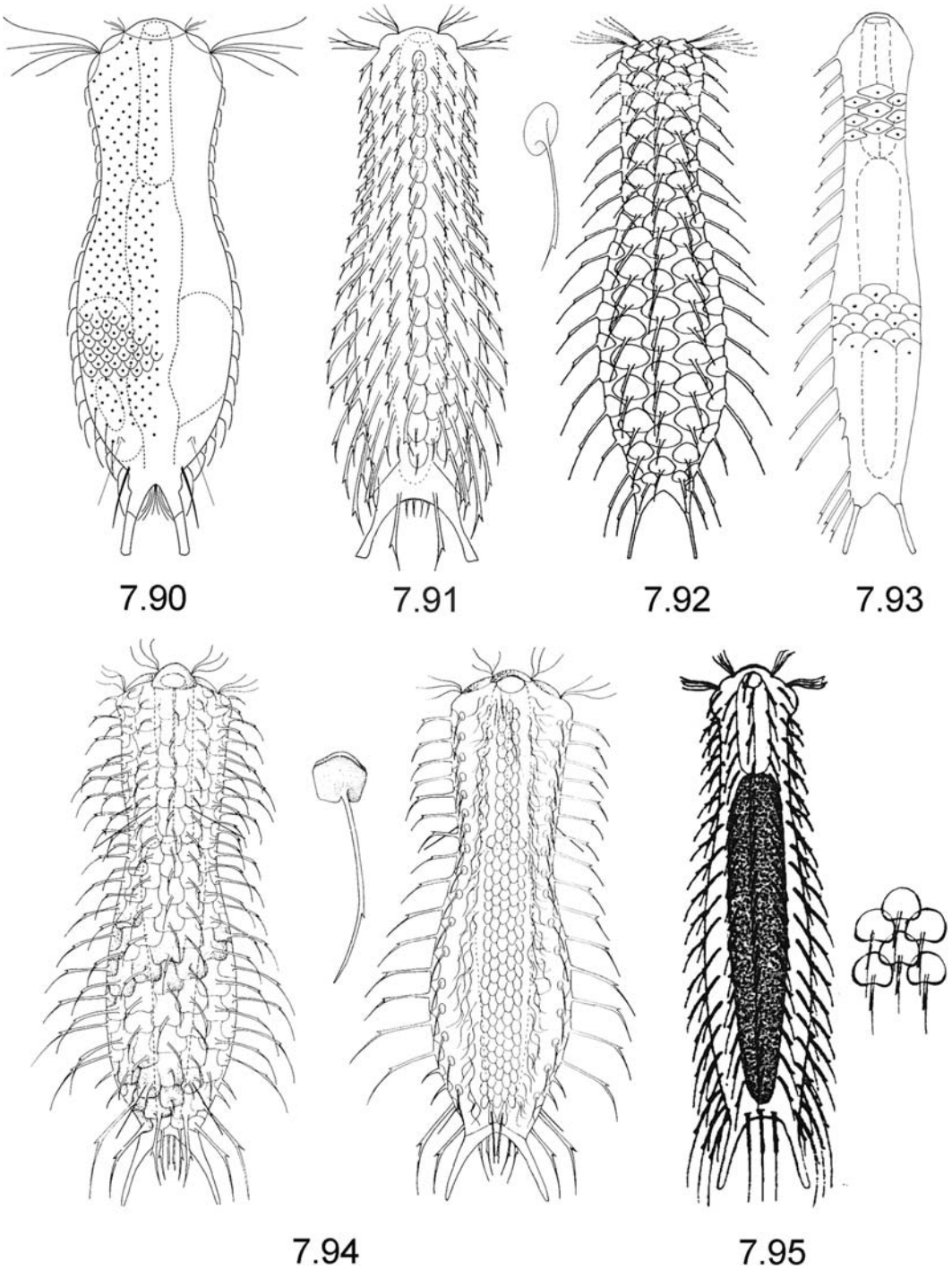


PLATE 20 Fig. 7.90 *Chaetonotus (Primochaetus) veronicae* Kånneby, 2013: dorsal view (redrawn from Kånneby, 2013); Fig. 7.91 *Chaetonotus (Primochaetus) chuni* Voigt, 1901: dorsal view with detail of a dorsal scale (from Balsamo, 1983 with permission); Fig. 7.92 *Chaetonotus (Primochaetus) armatus* Kisielewski, 1981: dorsal view (modified from Kisielewski, 1981); Fig. 7.93 *Chaetonotus (Primochaetus) scutulatus* Martin, 1981: schematic dorsal view (redrawn from Martin, 1981); Fig. 7.94 *Chaetonotus (Primochaetus) heideri* Brehm, 1917: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.95 *Chaetonotus (Primochaetus) cordiformis* Greuter, 1917: dorsal view with details of dorsal scales.

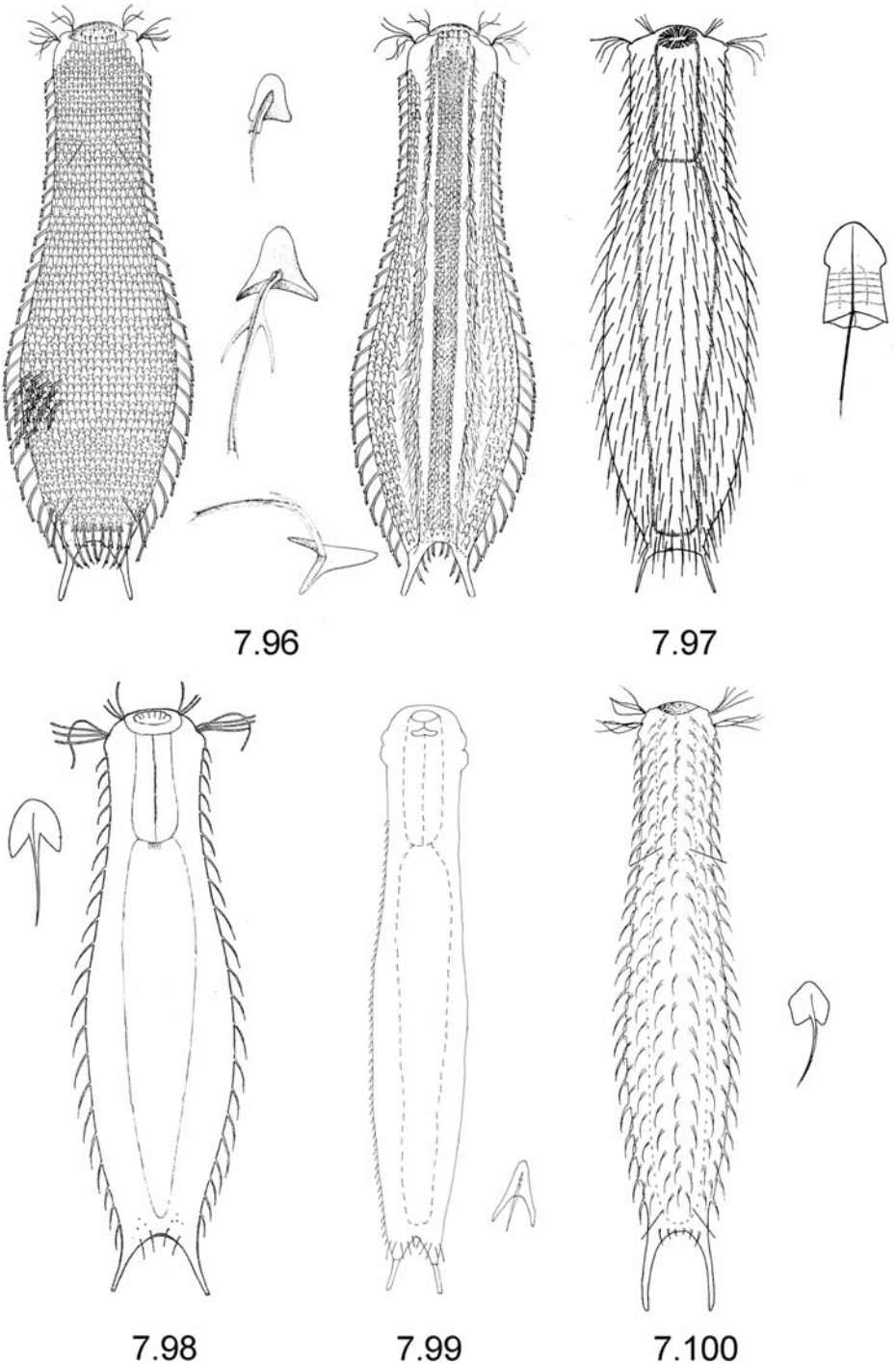


PLATE 21 Fig. 7.96 *Chaetonotus* (*Schizochaetonotus) schultzei* Metschnikoff, 1865: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.97 *Chaetonotus (Captochaetus) robustus* Davison, 1938: dorsal view with detail of a dorsal scale (from Kisielewski, 1979 with permission); Fig. 7.98 *Chaetonotus (Captochaetus) insigniformis* Greuter, 1917: dorsal view with detail of a dorsal scale (modified from Greuter, 1917); Fig. 7.99 *Chaetonotus (Captochaetus) segnis* Martin, 1981: schematic dorsal view with detail of a dorsal scale (redrawn from Martin, 1981); Fig. 7.100 *Chaetonotus (Captochaetus) simrothi* Voigt, 1909: dorsal view with detail of a dorsal scale (from Balsamo, 1983 with permission).

5′ Furca base spined; scales with unequal sides (Fig. 7.101) ..... *Chaetonotus arethusae* Balsamo & Todaro, 1995 [Italy, Sweden]

6(4) Caudal long spines on the dorsal posterior trunk 7

6′ No caudal long spines on the dorsal posterior trunk 9

7(6) Subtriangular scales with rounded lobes; three unpaired long dorsal intrafurcal spines 8

7′ Trilobate scales with very thin, pointed lobes; three paired long dorsal intrafurcal spines (Fig. 7.102) ..... *Chaetonotus rafalskii* Kisielewski, 1979 [Poland]

8(7) Several (18) small keeled scales on the dorsal posterior trunk; five dorsal intrafurcal spines; two paired long parafurcal spines (Fig. 7.103) ..... *Chaetonotus lancearis* Tretjakova, 1992 [Russia]

8′ Dorsal spined scales up to the caudal body end; three dorsal intrafurcal spines; one paired short parafurcal spine (Fig. 7.104) ..... *Chaetonotus tricuspidatus* Schwank, 1990 [Germany]

9(6) Dorsal subtriangular scales with rounded anterior lobe and large, diverging and truncated lateral lobes; furca base bare (Fig. 7.105) ..... *Chaetonotus jakubskii* Roszczak, 1936 [Poland]

9′ Subtriangular scales with rounded angles and two transversal keels, furca base with short spines (Fig. 7.106) ..... *Chaetonotus vorax* Remane, 1936 [Germany, Romania]

Gastrotricha: Chaetonotida: Chaetonotidae: *Chaetonotus* (*Chaetonotus*): Species

1 Dorsal spines short to medium length (<15−20 μm), of similar length along the body; posterior spines long as furca or shorter 2

1′ Dorsal spines long to very long (>15−20 μm) usually increasing in length posteriorly; posterior spines often longer than furca 39

2(1) Short, extremely fine, simple spines hardly visible; no apparent basal scales 3

2′ Distinct spines simple or barbed, of various length; usually distinct scales 4

3(2) Posterior trunk region distinctly narrowed, bearing long adhesive tubes strongly bent outwards; short, bent, extremely fine spines; no parafurcal spines (Fig. 7.107) ..... *Chaetonotus silvaticus* (Varga, 1963) [Hungary, Poland]

3′ Trunk cylindrical with straight adhesive tubes; body cuticle flexible, forming folds during locomotion; quite numerous, extremely short (2−3 μm) fine spines hardly visible giving a punctuate appearance; 1−2 paired long, simple parafurcal spines (Fig. 7.108) ..... *Chaetonotus vellosus* Martin, 1990 [United Kingdom]

4(2) Pharynx with two marked bulbs, the anterior containing paired hamulate and/or bacilliform cuticular structures 5

4′ Pharynx cylindrical or with 1−2 bulbs without cuticular structures 7

5(4) Dorsal triangular scales, one paired weak bacilliform cuticular structure in the anterior pharynx 6

5′ Dorsal rounded scales with two short, thin, pointed posterior lobes; four paired strongly hamulate cuticular structures in the anterior pharynx (Fig.7.109) ..... *Chaetonotus pawlowskii* Kisielewski, 1984 [Israel, Poland]

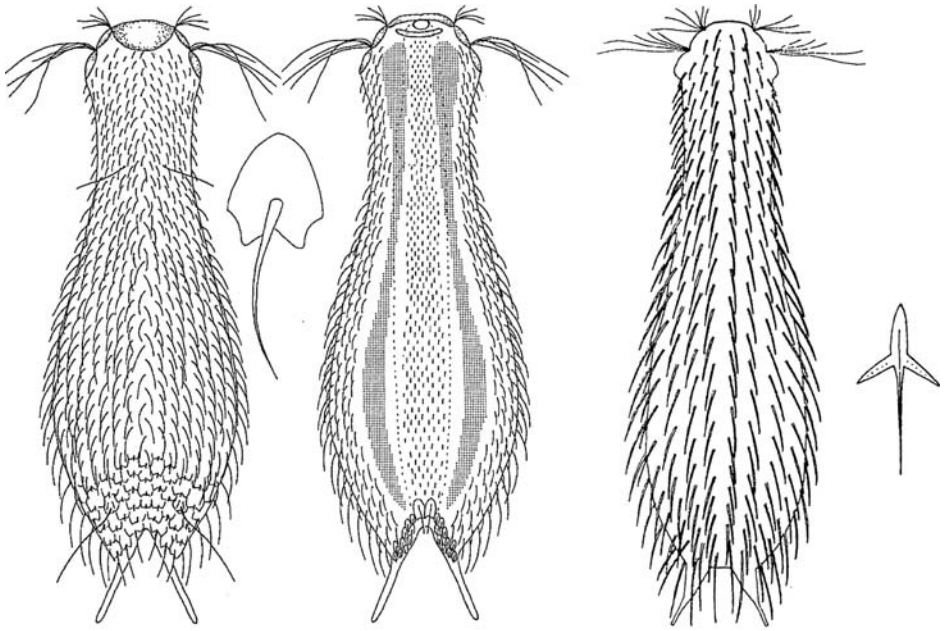
6(5) Adhesive tubes bent outwards; 22−26 columns of ∼30 scales (Fig. 7.110) ..... *Chaetonotus eximius* Kolicka, Kisielewski, Nesteruk, & Zawierucha, 2013 [Poland]

6′ Adhesive tubes straight; 15−17 columns of 17−18 scales (Fig. 7.111) ..... *Chaetonotus furcatus* Kisielewski, 1991 [Poland. Neotropics]

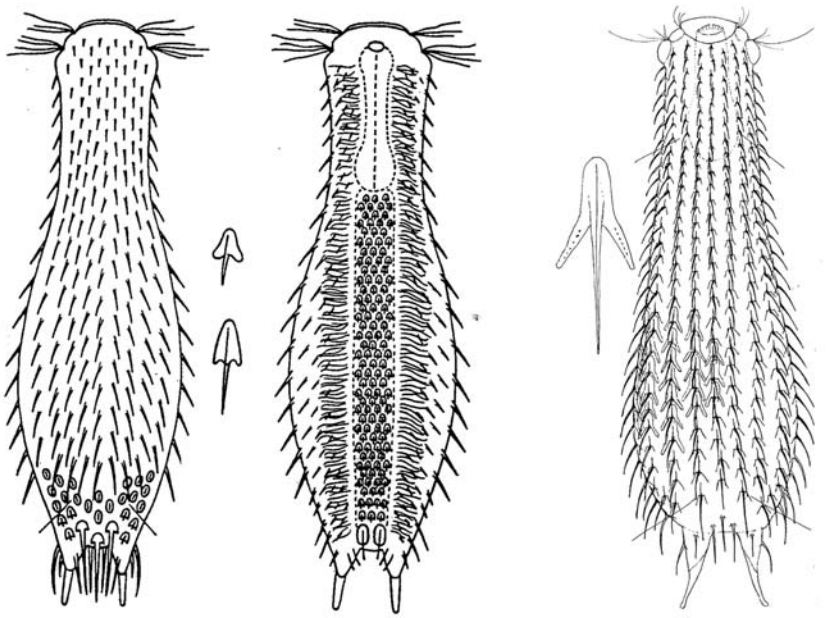
7(4) Dorsal trunk scales subtriangular or trilobate 8

7′ Dorsal trunk scales rounded, hemi-elliptical or hastate 21

8(5) Dorsal scales with posterior lobes different in shape from the anterior lobe; simple spines 9



7.101 7.102



7.103 7.104

PLATE 22 Fig. 7.101 *Chaetonotus (Captochaetus) arethusae* Balsamo & Todaro, 1995: dorsal and ventral views with detail of a dorsal scale (from Balsamo & Todaro, 1995 with permission); Fig. 7.102 *Chaetonotus (Captochaetus) rafalskii* Kisielewski, 1979: dorsal view with detail of a dorsal scale (from Kisielewski, 1979 with permission); Fig. 7.103 *Chaetonotus (Captochaetus) lancearis* Tretjakova, 1992: dorsal and ventral views with details of dorsal scales (modified from Tretjakova, 1992); Fig. 7.104 *Chaetonotus (Captochaetus) tricuspidatus* Schwank, 1990: dorsal view with detail of a dorsal scale (modified from Schwank, 1990).

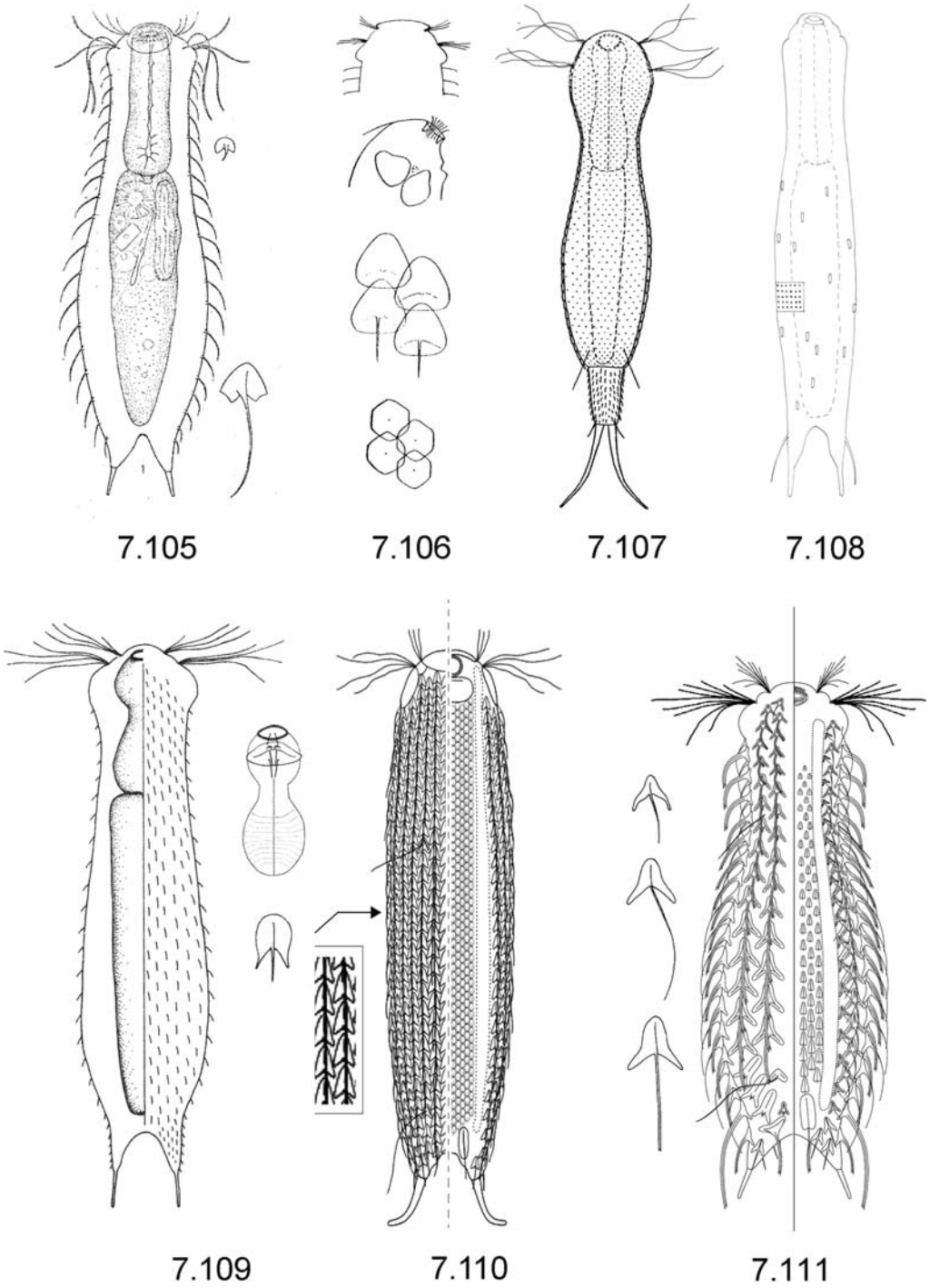


PLATE 23 Fig. 7.105 *Chaetonotus (Captochaetus) jakubskii* Roszczak, 1936: dorsal view with details of dorsal scales (from Roszczak, 1969 with permission); Fig. 7.106 *Chaetonotus (Captochaetus) vorax* Remane, 1936: dorsal and lateral view of the head with details of dorsal scales (modified from Remane, 1936); Fig. 7.107 *Chaetonotus (Chaetonotus) silvaticus* Varga, 1963: dorsal view (modified from Varga, 1963); Fig. 7.108 *Chaetonotus (Chaetonotus) vellosus* Martin, 1990: dorsal view (redrawn from Martin, 1990); Fig. 7.109 *Chaetonotus (Chaetonotus) pawlowski* Kisielewski, 1984: dorsal view with details of the pharynx and a dorsal scale (from Kisielewski, 1984 with permission); Fig. 7.110 *Chaetonotus (Chaetonotus) eximius* Kolicka, Kisielewski, Nesteruk, & Zawierucha, 2013: schematic composition of dorsal view (*left*) and ventral view (*right*) with a detail of dorsal scales (modified from Kolicka et al. 2013); Fig. 7.111 *Chaetonotus (Chaetonotus) furcatus* Kisielewski, 1991: schematic composition of dorsal view (*left*) and ventral view (*right*) (modified from Kolicka 2016).

8′ Dorsal scales with posterior lobes similar in shape to the anterior one; simple or barbed spines 15

9(8) Dorsal scales keeled and elongate, with very short posterior lobes; scales well-spaced out; spines extremely short (≤3 μm) 10

9′ Dorsal scales unkeeled and close to each other or partially overlapping; spines of medium length (≥3 μm) 11

10(9) Few columns of dorsal scales (seven), furca bare (Fig. 7.112) ..... *Chaetonotus scutatus* Saito, 1937 [Japan]

10′ Numerous columns of dorsal scales (17–21); furca scaled (Fig. 7.113) ..... *Chaetonotus naiadis* Balsamo & Todaro, 1995 [Italy, Sweden]

11(9) Dorsal trunk scales with rounded anterior lobe and pointed, narrow posterior lobes; 1–2 paired caudal spines or no caudal spines 12

11′ Dorsal trunk scales with rounded, wide anterior and posterior lobes; three paired long dorsal simple caudal spines, two of which are almost as long as the furca (Fig. 7.114) ..... *Chaetonotus venustus* d'Hondt, 1967 [France]

12(11) One or two paired long caudal spines; dorsal scales with large anterior lobe 13

12′ No long dorsal caudal spines, dorsal scales with small anterior lobe 14

13(12) Two paired long, thick, simple dorsal spines on the furca base; dorsal scales spaced, with sickle-shaped posterior lobes (Fig. 7.115) ..... *Chaetonotus disjunctus* Greuter, 1917 [Germany, Japan, Poland, Romania, Russia, Switzerland]

13′ One paired long, very thick, simple parafurcal spine; dorsal scales with subtriangular, pointed posterior lobes (Fig. 7.116) ..... *Chaetonotus puniceus* Martin, 1990 [United Kingdom]

14(12) Dorsal scales with very short posterior lobes; two ocelli; cylindrical pharynx (Fig. 7.117) ..... *Chaetonotus oculifer* Kisielewski, 1981 [Poland, Russia, Sweden]

14′ Dorsal scales with long, pointed posterior lobes; no ocelli; pharynx with strong posterior bulb (Fig. 7.118) ..... *Chaetonotus paluster* d'Hondt, 1967 [France]

15(8) Dorsal scales with anterior lobe much wider than posterior ones 16

15′ Dorsal scales with lobes clearly rounded, the anterior similar or slightly wider than posterior ones 18

16(15) Thick, simple spines with concave or blunt apex; scales with a long keel and long posterior lobes 17

16′ Barbed spines; scales with short posterior lobes slightly bent outwards; four short, thin dorsal caudal barbed spines protruding into the intrafurcal space (Fig. 7.119) ..... *Chaetonotus mitraformis* Greuter, 1917 [Germany, Poland, Romania, Switzerland]

17(16) Spines long (≥15 μm) arising from the body cuticle with an angle of 90°; three long dorsal intrafurcal spines with concave apex (Fig. 7.120) ..... *Chaetonotus murrayi* Remane, 1929 [Germany, Poland]

17′ Spines short (≤15 μm) arising obliquely from the body cuticle; no intrafurcal spines (Fig. 7.121) ..... *Chaetonotus quadratus* Martin, 1981 [United Kingdom]

18(15) One or two paired short parafurcal spines 19

18′ Three long, strong simple parafurcal spines; three lateral long simple caudal spines (Fig. 7.122) ..... *Chaetonotus* (*Chaetonotus*) *pravus* Kolicka, Kisielewski, Nesteruk, & Zawierucha, 2013 [Poland]

19(18) Dorsal spines uniform in thickness 20

19′ Trunk dorsal spines clearly thicker and distinct from the anterior ones; two short parafurcal simple spines; ventral field with small, rounded scales; two paired ventral, terminal keeled scales arranged in a transversal series (Fig. 7.123) ..... *Chaetonotus larus* (Müller, 1773) [Widespread]

20(19) Dorsal furca base with 4–5 paired spined scales; one paired long simple parafurcal spine (Fig. 7.124) ..... *Chaetonotus sphagnophilus* Kisielewski, 1981 [Poland, Russia, Sweden (?)]

20′ Dorsal furca base with some keeled scales; two paired short parafurcal spines (Fig. 7.125) ..... *Chaetonotus fluviatilis* Balsamo & Kisielewski, 1986 [Italy]

21(7) Dorsal trunk scales rounded or elliptical 22

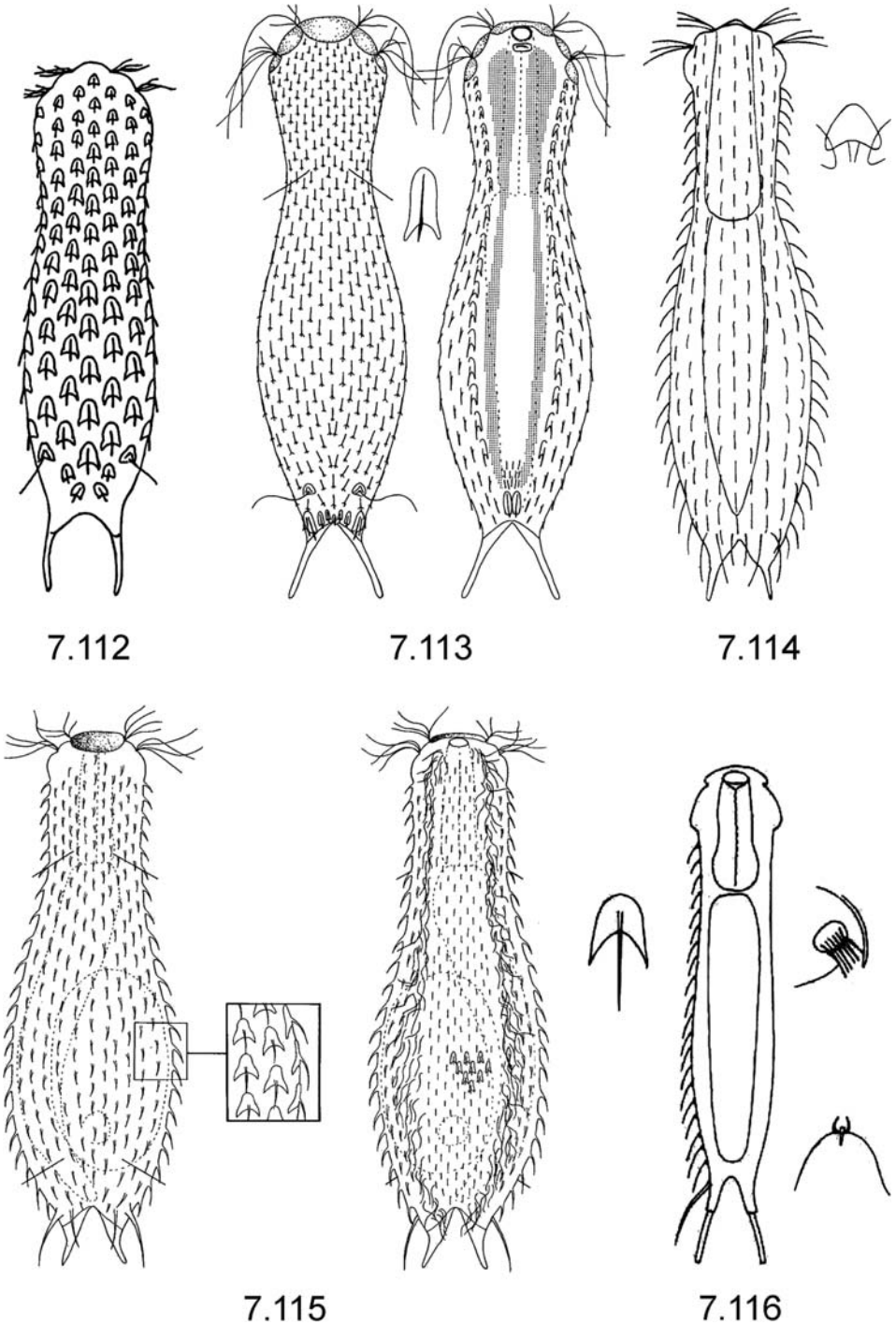


PLATE 24 Fig. 7.112 *Chaetonotus (Chaetonotus) scutatus* Saito, 1937: dorsal view (modified from Saito, 1937); Fig. 7.113 *Chaetonotus (Chaetonotus) naiadis* Balsamo & Todaro, 1995: dorsal and ventral views with detail of a dorsal scale (from Balsamo & Todaro, 1995 with permission); Fig. 7.114 *Chaetonotus (Chaetonotus) venustus* d'Hondt, 1967: dorsal view with a detail of dorsal scales (from d'Hondt, 1967 with permission); Fig. 7.115 *Chaetonotus (Chaetonotus) disjunctus* Greuter, 1917: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.116 *Chaetonotus (Chaetonotus) puniceus* Martin, 1990: dorsal view with details of the head (lateral view), the intrafurcal space and a dorsal scale (redrawn from Martin, 1990).

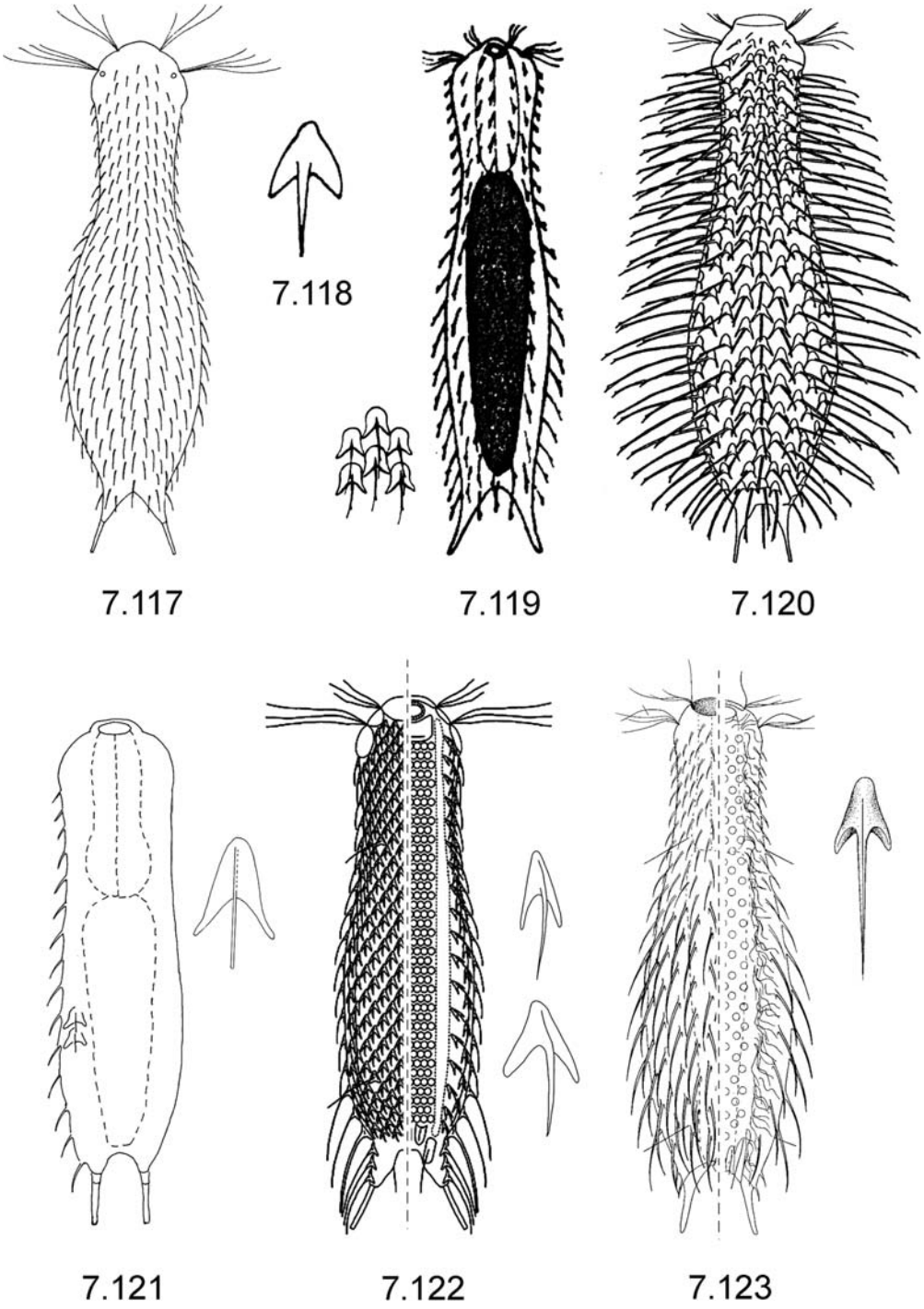
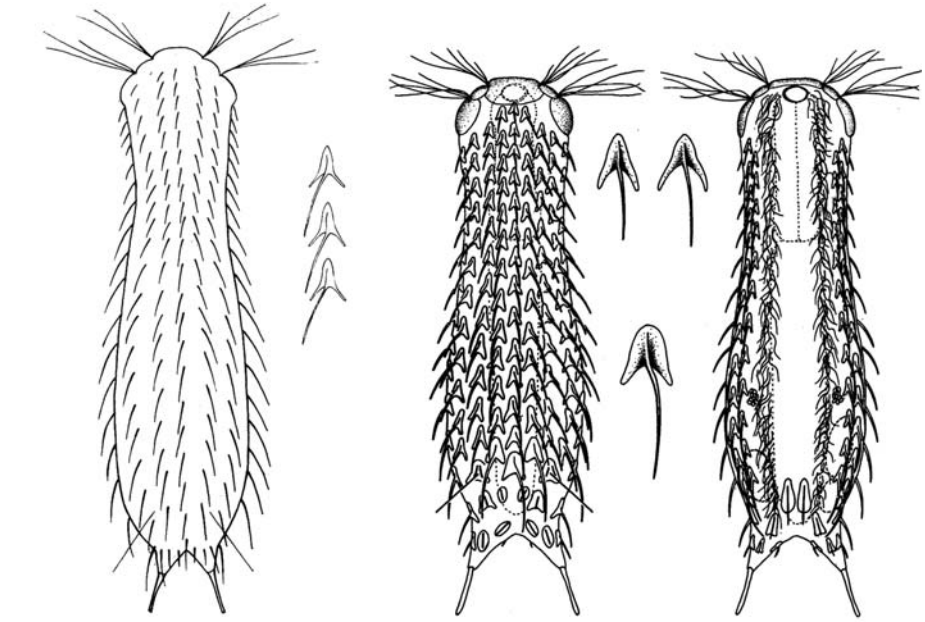
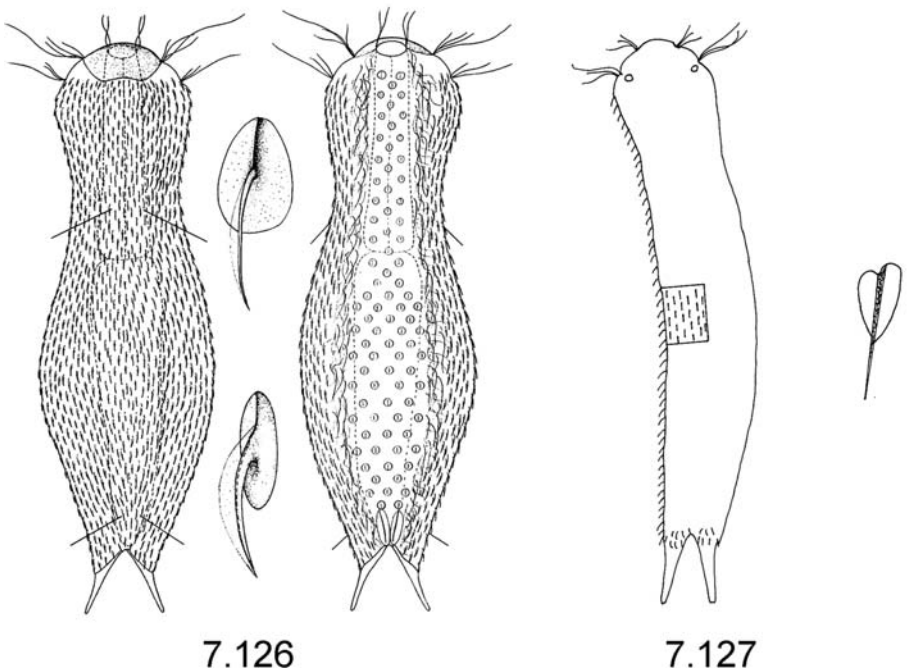


PLATE 25 Fig. 7.117 *Chaetonotus (Chaetonotus) oculifer* Kisielewski, 1981: dorsal view (modified from Kisielewski, 1981); Fig. 7.118 *Chaetonotus (Chaetonotus) paluster* d'Hondt, 1967: detail of a dorsal scale (from d'Hondt, 1967 with permission); Fig. 7.119 *Chaetonotus (Chaetonotus) mitraformis* Greuter, 1917: dorsal view with details of dorsal scales (modified from Greuter, 1917); Fig. 7.120 *Chaetonotus (Chaetonotus) murrayi* Remane, 1929: dorsal view (modified from Remane, 1929); Fig. 7.121 *Chaetonotus (Chaetonotus) quadratus* Martin, 1981: dorsal view with detail of a dorsal scale (redrawn from Martin, 1981); Fig. 7.122 *Chaetonotus (Chaetonotus) pravus* Kolicka, Kisielewski, Nesteruk, & Zawierucha, 2013: schematic composition of dorsal view (*left*) and ventral view (*right*) with a detail of dorsal scales (modified from Kolicka et al. 2013); Fig. 7.123 *Chaetonotus (Chaetonotus) larus* Müller, 1773: composition of dorsal and ventral views with detail of a dorsal scale (from Balsamo, 1983 with permission).



7.124 7.125



7.126 7.127

PLATE 26 Fig. 7.124 *Chaetonotus (Chaetonotus) sphagnophilus* Kisielewski, 1981: dorsal view with detail of dorsal scales (modified from Kisielewski, 1981); Fig. 7.125 *Chaetonotus (Chaetonotus) fluviatilis* Balsamo & Kisielewski, 1986: dorsal and ventral views with details of dorsal scales (from Balsamo & Kisielewski, 1986 with permission); Fig. 7.126 *Chaetonotus (Chaetonotus) lunatospinosus* Balsamo, 1981: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.127 *Chaetonotus (Chaetonotus) splendidus* Preobrajenskaia, 1926: dorsal view with detail of a dorsal scale (redrawn from Preobrajenskaia, 1926).

21′ Dorsal trunk scales hemi-elliptical or hastate, posteriorly concave 24

22(21) Dorsal scales in <35 columns; spines without lamellar expansion; furca base bare 23

22′ Dorsal scales in >35 columns; scales suboval with spines bent and provided with a lamellar expansion; furca base scaled (Fig. 7.126) ..... *Chaetonotus lunatospinosus* Balsamo, 1981
[Italy]

23(22) Eleven to 13 dorsal columns of 40−45 cordate, keeled scales; two ocelli (Fig. 7.127) ..... *Chaetonotus splendidus* Preobrajenskaia, 1926
[Russia]

23′ Nine dorsal columns of 18−20 elliptical, unkeeled scales; no ocelli (Fig. 7.128) ..... *Chaetonotus beauchampi* d'Hondt, 1967
[France]

24(21) Dorsal scales in <13 columns 25

24′ Dorsal scales in ≥13 columns 28

25(24) Three to five long dorsal intrafurcal spines; no parafurcal spines 26

25′ No long dorsal intrafurcal spines; 2−3 paired short parafurcal spines 27

26(25) Five dorsal intrafurcal spines, much longer than trunk spines; 11 dorsal columns of ∼40 scales (Fig. 7.129) ..... *Chaetonotus stagnalis* d'Hondt, 1967
[France]

26′ Three to five dorsal intrafurcal spines longer than trunk spines; 9 or 10 columns of 45−55 scales; hastate scales with very long posterior lobes (∼1/2 scale length), slightly converging medially (Fig. 7.130) ..... *Chaetonotus alatus* Schwank, 1990

27(25) Dorsal scales elongate, hemi-elliptical in 11 columns; two large ocelli; cylindrical, thin pharynx (Fig. 7.131) ..... *Chaetonotus oculatus* Schwank, 1990
[Germany]

27′ Dorsal scales hastate in 11−13 columns; no ocelli; thick pharynx enlarged posteriorly (Fig. 7.132) ..... *Chaetonotus brevispinosus* Zelinka, 1889
[Europe]

28(24) Trilobate head with large kephalion and epipleuria; hastate, ogival scales 29

28′ Pentalobate head with plates of similar size; hemi-elliptical scales deeply concave 31

29(28) Elongate or fusiform body; head wide as the trunk or narrower; normal or short furca (1/8−1/10 of body length) 30

29′ Very slender body; head wider than the trunk; long furca (up to 1/5 of body length) (Fig. 7.133) ..... *Chaetonotus greuteri* Remane, 1927
[Germany, Israel (?), Poland, Romania, Switzerland]

30(29) Elongate body with distinct head; 5−8 paired dorsal long spines protruding into the intrafurcal space; 21−25 columns of 55−60 spined scales (Fig. 7.134) ..... *Chaetonotus christianus* Schwank, 1990
[Germany]

30′ Stout, fusiform body with small head; 3−4 paired dorsal terminal spines; 10−12 columns of 31 or 32 spined scales (Fig. 7.135) ..... *Chaetonotus linguaeformis* Voigt, 1902
[Bulgaria, Germany, Poland, Romania]

31(28) Spines very short (<2 μm); no long spines on the dorsal furca base 32

31′ Spines short (2−10 μm); long spines on the dorsal furca base 35

32(31) Dorsal scales in ≤19 columns; rounded or hastate scales slightly concave 33

32′ Dorsal scales in ≥31 columns; elongate, hemi-elliptical keeled scales deeply concave with long posterior lobes; thin, very bent simple spines (Fig. 7.136) ..... *Chaetonotus daphnes* Balsamo & Todaro, 1995
[Italy, Sweden]

33(32) Dorsal scales in 13 columns; furca base scaled 34

33′ Dorsal rounded scales in 17−19 columns; furca base bare (Fig. 7.137) ..... *Chaetonotus multispinosus* Grünspan, 1908
[Widespread]

34(33) Rounded scales posteriorly concave; cylindrical pharynx (Fig. 7.138) ..... *Chaetonotus minimus* Marcolongo, 1910
[Italy]

34′ Hastate scales; pharynx with two bulbs, the posterior one especially strong (Fig. 7.139) ..... *Chaetonotus poznaniensis* Kisielewski, 1981
[Poland]

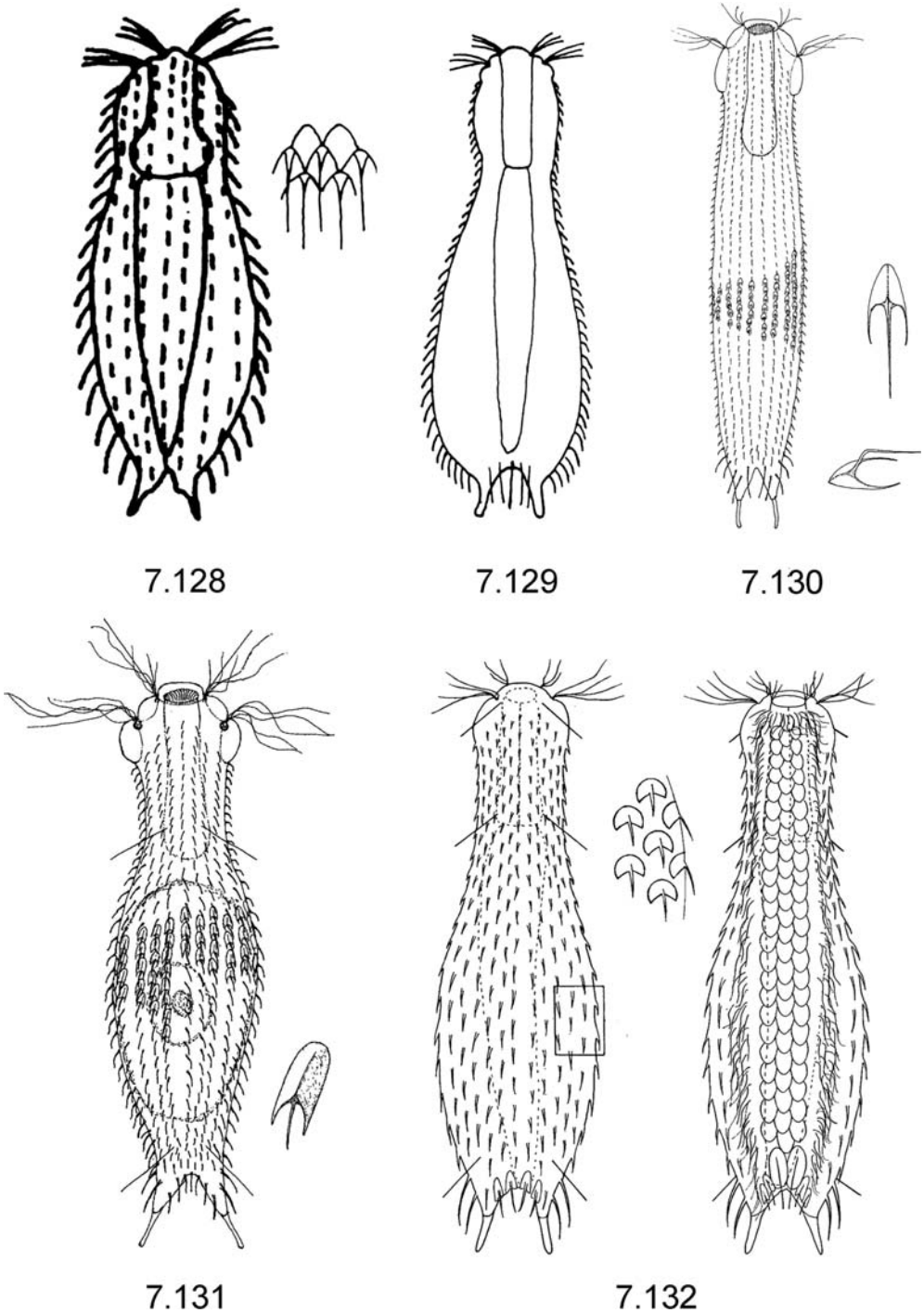
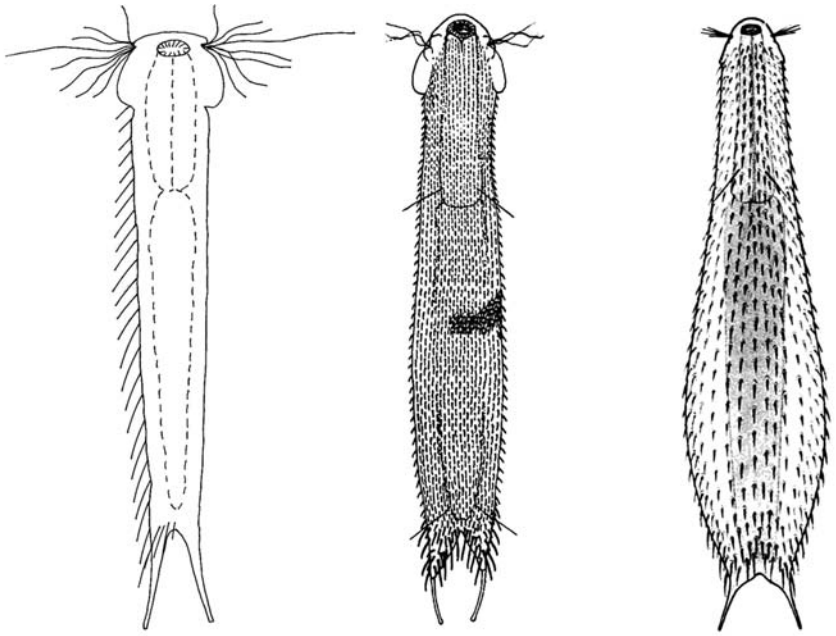
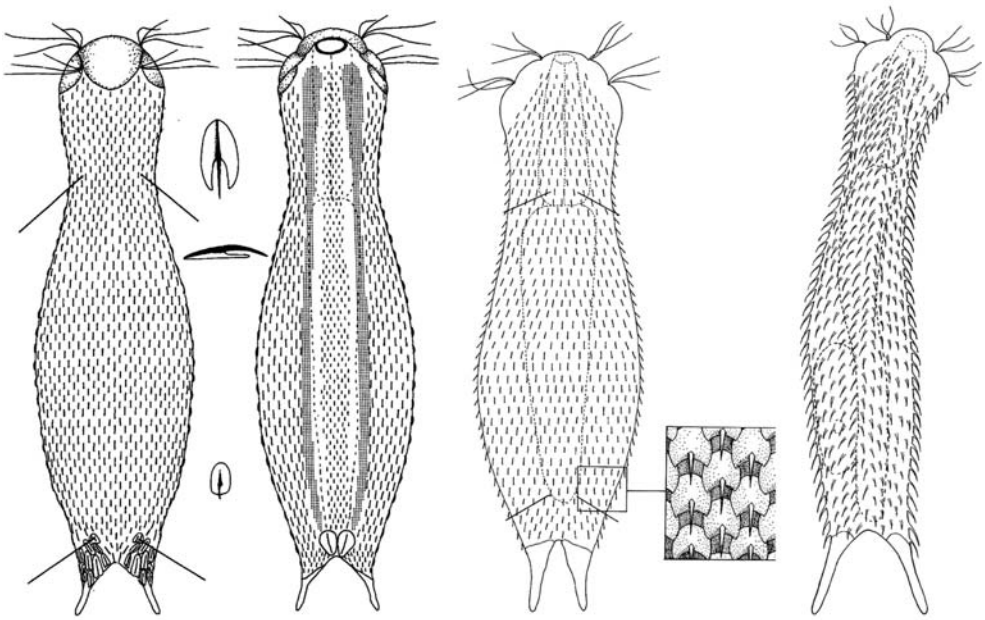


PLATE 27 Fig. 7.128 *Chaetonotus (Chaetonotus) beauchampi* d'Hondt, 1967: dorsal view with details of dorsal scales (from d'Hondt, 1967 with permission); Fig. 7.129 *Chaetonotus (Chaetonotus) stagnalis* d'Hondt, 1967: schematic dorsal view (from d'Hondt, 1967 with permission); Fig. 7.130 *Chaetonotus (Chaetonotus) alatus* Schwank, 1990: dorsal view with details of dorsal scales (from Schwank, 1990 with permission); Fig. 7.131 *Chaetonotus (Chaetonotus) oculatus* Schwank, 1990: dorsal view with detail of a dorsal scale (modified from Schwank 1990); Fig. 7.132 *Chaetonotus (Chaetonotus) brevispinosus* Zelinka, 1889: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission).



7.133 7.134 7.135



7.136 7.137 7.138

PLATE 28 Fig. 7.133 *Chaetonotus (Chaetonotus) greuteri* Remane, 1927: dorsal view (modified from Remane, 1927); Fig. 7.134 *Chaetonotus (Chaetonotus) christianus* Schwank, 1990: dorsal view (from Schwank, 1990 with permission); Fig. 7.135 *Chaetonotus (Chaetonotus) linguaeformis* Voigt, 1902: dorsal view (modified from Voigt, 1904); Fig. 7.136 *Chaetonotus (Chaetonotus) daphnes* Balsamo & Todaro, 1995: dorsal and ventral views with details of dorsal scales (from Balsamo & Todaro, 1995 with permission); Fig. 7.137 *Chaetonotus (Chaetonotus) multispinosus* Grünspan, 1908: dorsal view with detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.138 *Chaetonotus (Chaetonotus) minimus* Marcolongo, 1910: dorsal view (from Balsamo, 1983 with permission).

35(31) Hemi-elliptical scales with short, broad posterior lobes 36

35′ Hemi-elliptical, very elongate scales with lobes long up to 1/3 scale length, diverging externally; 2−3 paired short, simple spines on the dorsal furca base; one paired long, simple parafurcal spine (Fig. 7.140) ..... *Chaetonotus elegans* Konsuloff, 1921
[Bulgaria, Germany, Hungary, Romania]

36(35) Two to five paired dorsal long, simple spines on the furca base; no parafurcal spines; ventral field with numerous small keeled or smooth scales 37

36′ One paired long, simple spine on the dorsal furca base; one paired long parafurcal thick simple spine; ventral field with large smooth plates anteriorly and posteriorly keeled (Fig. 7.141) ..... *Chaetonotus microchaetus* Preobrajenskaia, 1926
[Italy, Poland, Russia, Sweden]

37(36) No dorsal long spines on the trunk; keeled scales 38

37′ Five dorsal long, simple spines arranged in a transversal series on the mid trunk; furcal base with two paired spines; scales unkeeled (Fig. 7.142) ..... *Chaetonotus crassus* Preobrajenskaia, 1926
[Romania, Russia]

38(37) Pentalobate head; ∼60 scales per column; straight spines ≤10 μm long (Fig. 7.143) ..... *Chaetonotus polyspinosus* Greuter, 1917
[Germany, Italy, Israel, Korea, Poland, Romania, Russia, Sweden, Switzerland, United Kingdom]

38′ Trilobate head; ∼40 scale per column; straight spines very thick and short (≤4 μm) (Fig. 7.144) ..... *Chaetonotus retiformis* Suzuki & Furuya, 2011
[Japan]

39(1) Several dorsal trunk spines clearly distinct from the anterior ones for their much greater length and thickness; long trunk dorsal spines simple or barbed 40

39′ Dorsal spines gradually increasing in length posteriorly; dorsal spines simple, barbed or with concave apex 65

40(39) Dorsal trunk long spines in various number and arrangement; basal scales usually present 41

40′ Six dorsal trunk long spines with lamellar shape, within a group of 14 spines arranged in eight series; very reduced basal scales, trilobate in shape (Fig. 7.145) ..... *Chaetonotus lucksi* Voigt, 1958
[Germany]

41(40) Dorsal trunk long spines inserted on triangular scales; dorsal short spines simple or barbed 42

41′ Dorsal trunk long spines inserted on rounded, hemi-elliptical, or hastate scales; dorsal short spines simple 51

42(41) Dorsal scales distinct 43

42′ Dorsal scales reduced or not apparent 49

43(42) Dorsal spines simple 44

43′ Dorsal spines barbed 45

44(43) Four thick spines relatively long on the posterior trunk; no parafurcal spines; ventral field with small round scales (Fig. 7.146) ..... *Chaetonotus benacensis* Balsamo & Fregni, 1995
[Italy, Sweden]

44′ Three long thick spines on the posterior trunk; two paired long parafurcal spines; ventral field bare (Fig. 7.147) ..... *Chaetonotus trispinosus* Balsamo, 1990
[Italy]

45(43) One or two dorsal spines of intermediate length between the short anterior spines and the long trunk spines 46

45′ Sharp difference in length between short anterior spines and long trunk spines 47

46(45) Ventral interciliary field with keeled scales (Fig. 7.148) ..... *Chaetonotus hystrix* Metschnikoff, 1865
[Widespread]

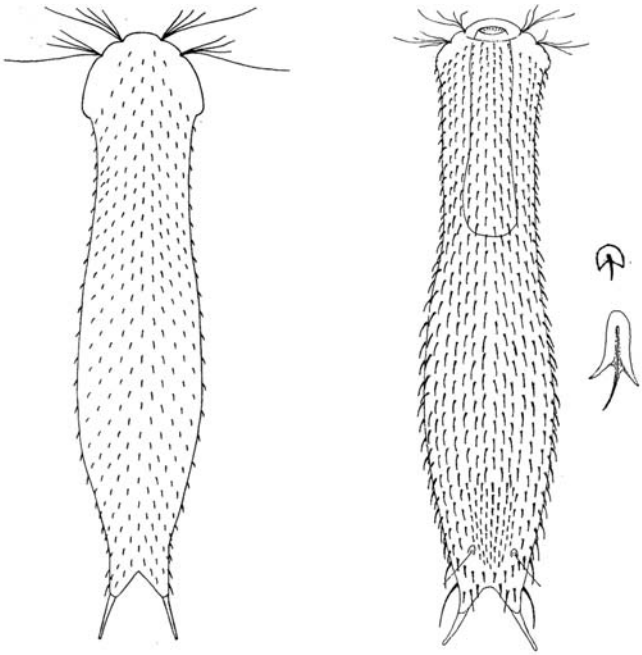
46′ Ventral interciliary field with smooth scales (Fig. 7.149) ..... *Chaetonotus machikanensis* Suzuki & Furuya, 2011
[Japan]

47(45) Trunk with a distinct dorsal group of 16−18 very long spines 48

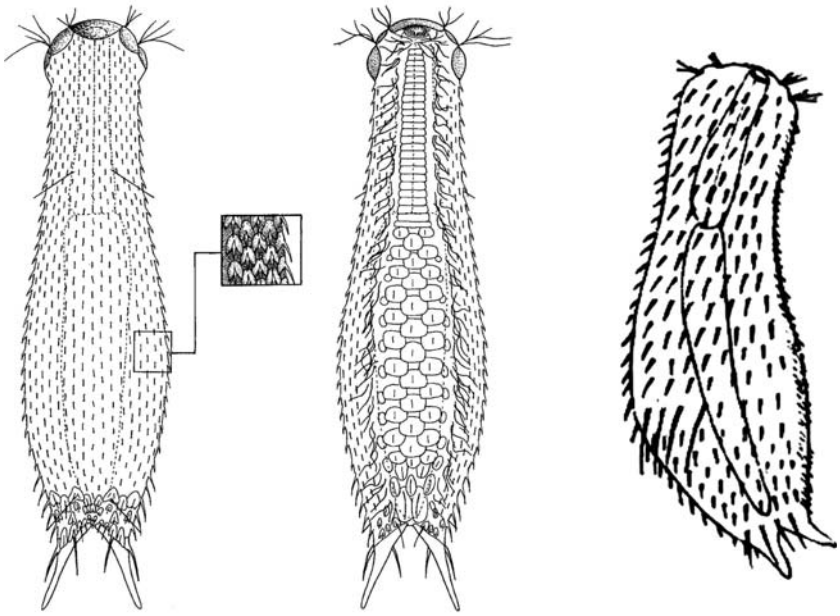
47′ Trunk with a distinct dorsal group of 25−27 very long spines (Fig. 7.150) ..... *Chaetonotus macrochaetus* Zelinka, 1889
[Widespread. Nearctic, Neotropics]

48(47) Large body size (≥140 μm); dorsal very long spines on the trunk (60−70 μm) (Fig. 7.151) ..... *Chaetonotus euhystrix* Schwank, 1990
[Germany, Sweden]

48′ Small body size (≤100 μm); trunk spines of medium length (15−19 μm); trunk dorsal scales with a clear bulge along the anterior edges (Fig. 7.152) ..... *Chaetonotus persetosus* Zelinka, 1889
[Widespread]



7.139 7.140



7.141 7.142

PLATE 29 Fig. 7.139 *Chaetonotus (Chaetonotus) poznaniensis* Kisielewski, 1981: dorsal view (modified from Kisielewski, 1981); Fig. 7.140 *Chaetonotus (Chaetonotus) elegans* Konsuloff, 1921; dorsal view with details of dorsal scales (modified from Konsuloff, 1921); Fig. 7.141 *Chaetonotus (Chaetonotus) microchaetus* Preobrajenskaia, 1926: dorsal and ventral views with detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.142 *Chaetonotus (Chaetonotus) crassus* Preobrajenskaia, 1926: dorsal view (modified from Preobrajenskaia, 1926.

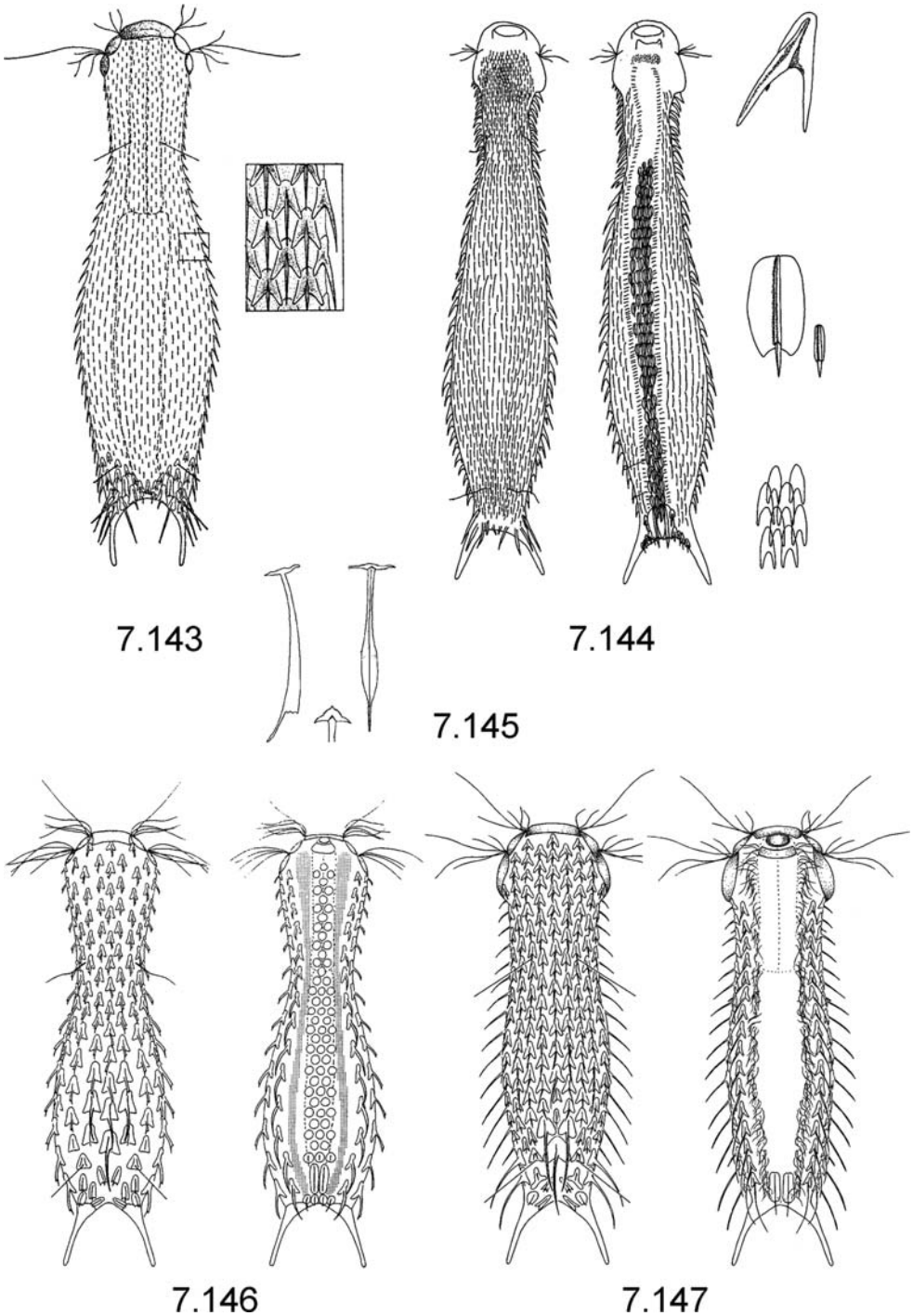
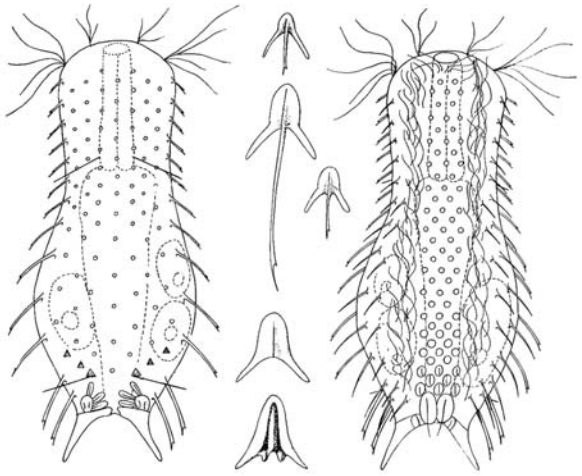
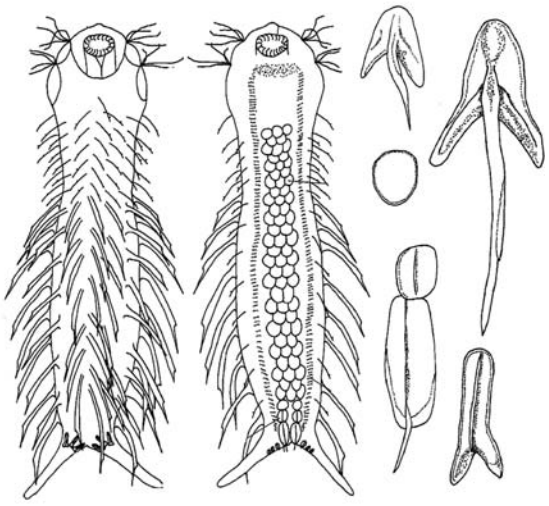


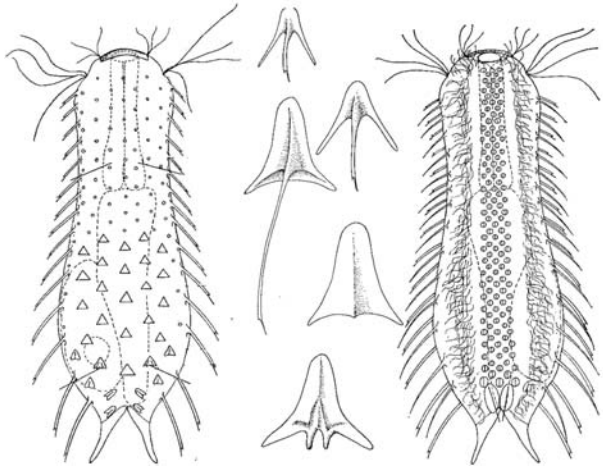
PLATE 30 Fig. 7.143 *Chaetonotus (Chaetonotus) polyspinosus* Greuter, 1917: dorsal view with detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.144 *Chaetonotus (Chaetonotus) retiformis* Suzuki & Furuya, 2011: dorsal and ventral views with detail of dorsal scales (from Suzuki & Furuya, 2011 with permission); Fig. 7.145 *Chaetonotus (Chaetonotus) lucksi* Voigt, 1958: detail of dorsal scales and spines (modified from Voigt, 1958); Fig. 7.146 *Chaetonotus (Chaetonotus) benacensis* Balsamo & Fregni, 1995: dorsal and ventral views (from Balsamo & Fregni, 1995 with permission); Fig. 7.147 *Chaetonotus (Chaetonotus) trispinosus* Balsamo, 1990: dorsal and ventral views (from Balsamo, 1990 with permission).



7.148



7.149



7.150

PLATE 31 Fig. 7.148 *Chaetonotus (Chaetonotus) hystrix* Metschnikoff, 1865: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.149 *Chaetonotus (Chaetonotus) machikanensis* Suzuki & Furuya, 2011: dorsal and ventral views with details of dorsal and ventral scales (from Suzuki & Furuya, 2011 with permission); Fig. 7.150 *Chaetonotus (Chaetonotus) macrochaetus* Zelinka, 1889: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission).

49(42) Scales not apparent 50

49′ Scales reduced; 13 long dorsal spines on the trunk; one paired parafurcal spine (Fig. 7.153) ..... *Chaetonotus fujisanensis* Sudzuki, 1971
[Japan]

50(49) Trunk with 25 long, dorsal spines; one paired parafurcal spine (Fig. 7.154) ..... *Chaetonotus acanthophorus* Stokes, 1887
[Spain, Italy]

50′ Trunk with 13 long, dorsal spines; two paired parafurcal spines (Fig. 7.155) ..... *Chaetonotus enormis* Stokes, 1887
[Italy]

51(41) Long dorsal spines simple 52

51′ Long dorsal spines barbed 53

52(51) Trunk with five paired very long dorsal spines, arranged into two columns; the most posterior spines much longer than furca; short dorsal simple spines (Fig. 7.156) ..... *Chaetonotus decemsetosus* Marcolongo, 1910
[Italy]

52′ Trunk with six long, dorsal spines inserted on scale rudiments on mid trunk, arranged into two transverse series; small rounded dorsal scales with no spines; thin, simple lateral spines (Fig. 7.157) ..... *Chaetonotus vargai* Rudescu, 1967
[Hungary, Romania]

53(51) Long dorsal spines with enlarged base or rudimental basal scale 54

53′ Long dorsal spines with distinct basal scale 59

54(53) Dorsal scales not apparent or absent 55

54′ Dorsal scales present on the whole body 57

55(54) Four to eight barbed dorsal spines arranged into 2−3 series on the trunk; fine scales and/or spines on the body 56

55′ Five long barbed dorsal spines arranged into two series on the mid trunk; no scales or other spines (Fig. 7.158) ..... *Chaetonotus quintospinosus* Greuter, 1917
[Poland, Switzerland]

56(55) Seven or eight very long barbed spines arranged into two series, the posterior ones very long (up $^{1}/_{2}$ body length), and reaching the furca; fine lateral spines (Fig. 7.159) ..... *Chaetonotus longispinosus* Stokes, 1887
[Widespread]

56′ Four to eight long barbed spines arranged into 2−3 series, long ∼1/5 body length; fine lateral spines with enlarged bases (Fig. 7.160) ..... *Chaetonotus spinulosus* Stokes, 1887
[Widespread]

57(54) Nine very long barbed spines (≥1/3 body length) arranged in three columns on the anterior trunk; keeled and/or spined scales on the whole body; two series of thick spines on the head 58

57′ Nine long barbed spines (≤1/3 body length) with small basal scales arranged in three columns on the mid trunk; small scales covering the whole body, except for an elliptical dorsal area on the head; a series of dorsal spines on the head (Fig. 7.161) ..... *Chaetonotus trilineatus* Valkanov, 1937
[Bulgaria (?), Romania]

58(57) Dorsal spines barbed, long ∼1/3 body length (Fig. 7.162) ..... *Chaetonotus novenarius* Greuter, 1917
[Switzerland]

58′ Dorsal spines double-barbed, long 2/3 of body length (Fig. 7.163) ..... *Chaetonotus balsamoae* Kisielewski, 1998
[Italy, Poland]

59(53) Long dorsal spines with triangular or polygonal basal scales 60

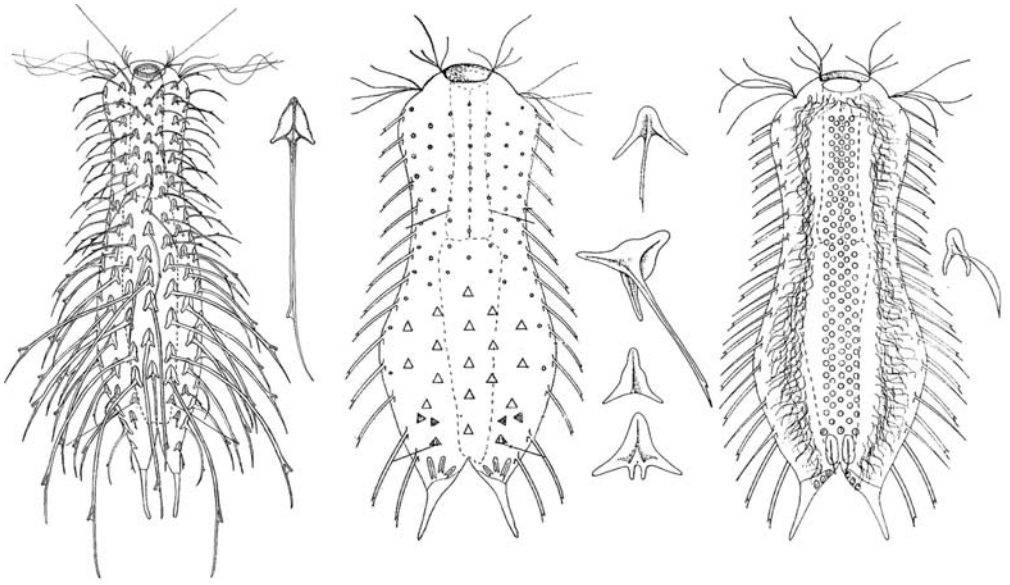
59′ Long dorsal spines with rounded or hemi-elliptical scales posteriorly concave 61

60(59) Seven to nine long dorsal, barbed spines in three columns; basal scales triangular; dorsal head with no scale or spine (Fig. 7.164) ..... *Chaetonotus aemilianus* Balsamo, 1978
[Italy, Sweden]

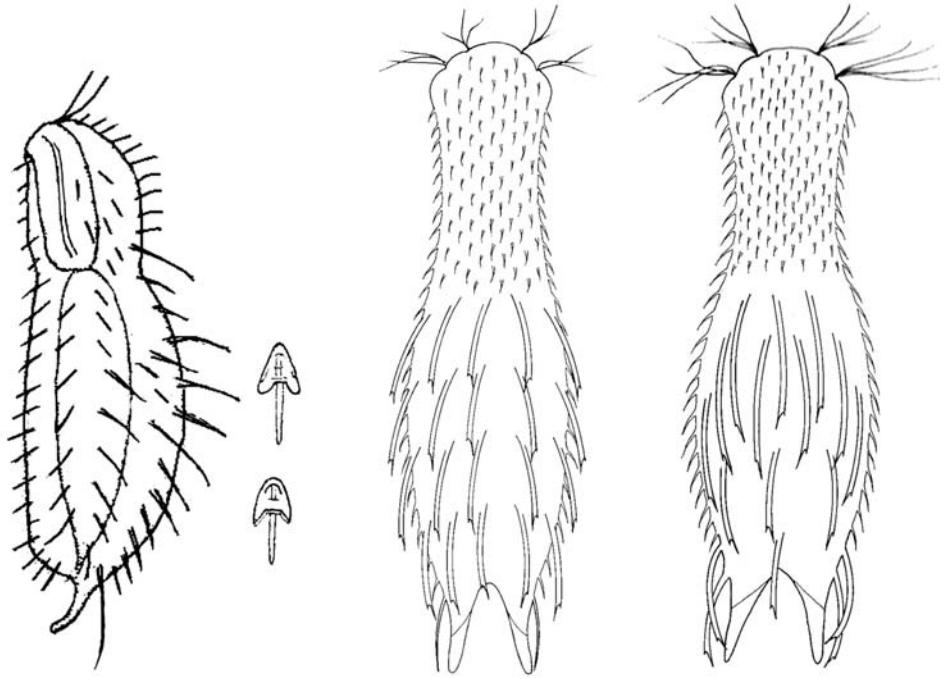
60′ Five long, thick, dorsal barbed spines in two series; basal scales pentagonal or polygonal; dorsal head with spined scales (Fig. 7.165) ..... *Chaetonotus ferrarius* Schwank, 1990
[Germany]

61(59) Small body size (≤120 μm); ≤8 dorsal long, barbed spines arranged in a group on the mid trunk; no parafurcal spines 62

61′ Large body size (≥200 μm); eight dorsal long, barbed spines arranged in a series on the mid trunk; one paired, barbed parafurcal spine longer than the furca; rounded scales posteriorly concave (Fig. 7.166) ..... *Chaetonotus heterochaetus* Daday, 1905
[Russia]



7.151 7.152



7.153 7.154 7.155

PLATE 32 Fig. 7.151 *Chaetonotus (Chaetonotus) euhystrix* Schwank, 1990: dorsal view with detail of a dorsal scale (from Schwank, 1990 with permission); Fig. 7.152 *Chaetonotus (Chaetonotus) persetosus* Zelinka, 1889: dorsal and ventral views with details of dorsal and ventral scales (from Balsamo, 1983 with permission); Fig. 7.153 *Chaetonotus (Chaetonotus) fujisanensis* (Sudzuki, 1971): lateral view with detail of dorsal scales (modified from Sudzuki, 1971); Fig. 7.154 *Chaetonotus (Chaetonotus) acanthophorus* Stokes, 1887: dorsal view (from Balsamo, 1983 with permission); Fig. 7.155 *Chaetonotus (Chaetonotus) enormis* Stokes, 1887: dorsal view (from Balsamo, 1983 with permission).

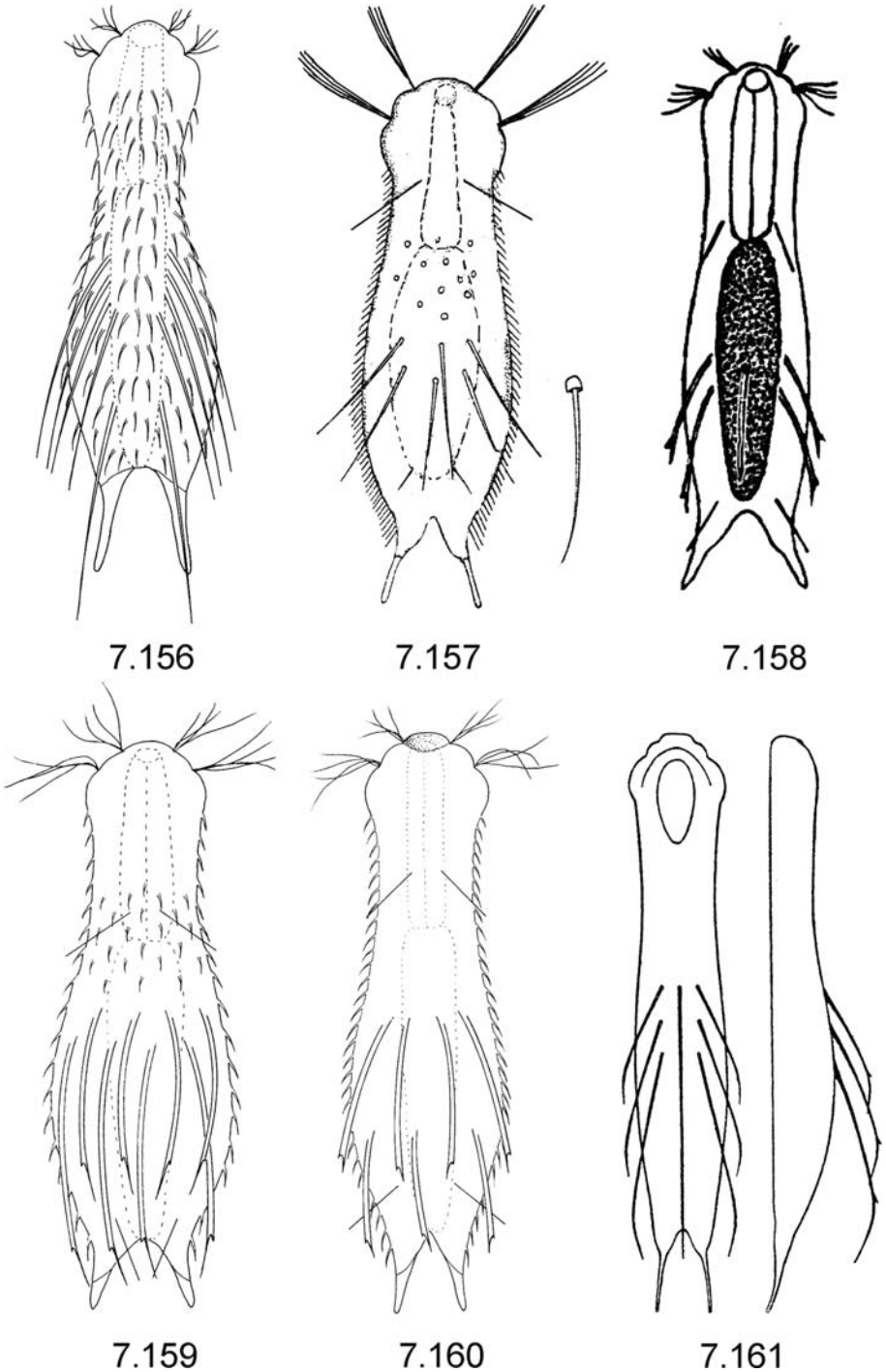


PLATE 33 Fig. 7.156 *Chaetonotus (Chaetonotus) decemsetosus* Marcolongo, 1910: dorsal view (from Balsamo, 1990 with permission); Fig. 7.157 *Chaetonotus (Chaetonotus) vargai* Rudescu, 1967: dorsal view and a detail of a dorsal scale (modified from Rudescu, 1967); Fig. 7.158 *Chaetonotus (Chaetonotus) quintospinosus* Greuter, 1917: dorsal view (modified from Greuter, 1917); Fig. 7.159 *Chaetonotus (Chaetonotus) longispinosus* Stokes, 1887: dorsal view (from Balsamo, 1983 with permission); Fig. 7.160 *Chaetonotus (Chaetonotus) spinulosus* Stokes, 1887: dorsal view (from Balsamo, 1983 with permission); Fig. 7.161 *Chaetonotus (Chaetonotus) trilineatus* Valkanov, 1937: dorsal and lateral views (modified from Valkanov, 1937).

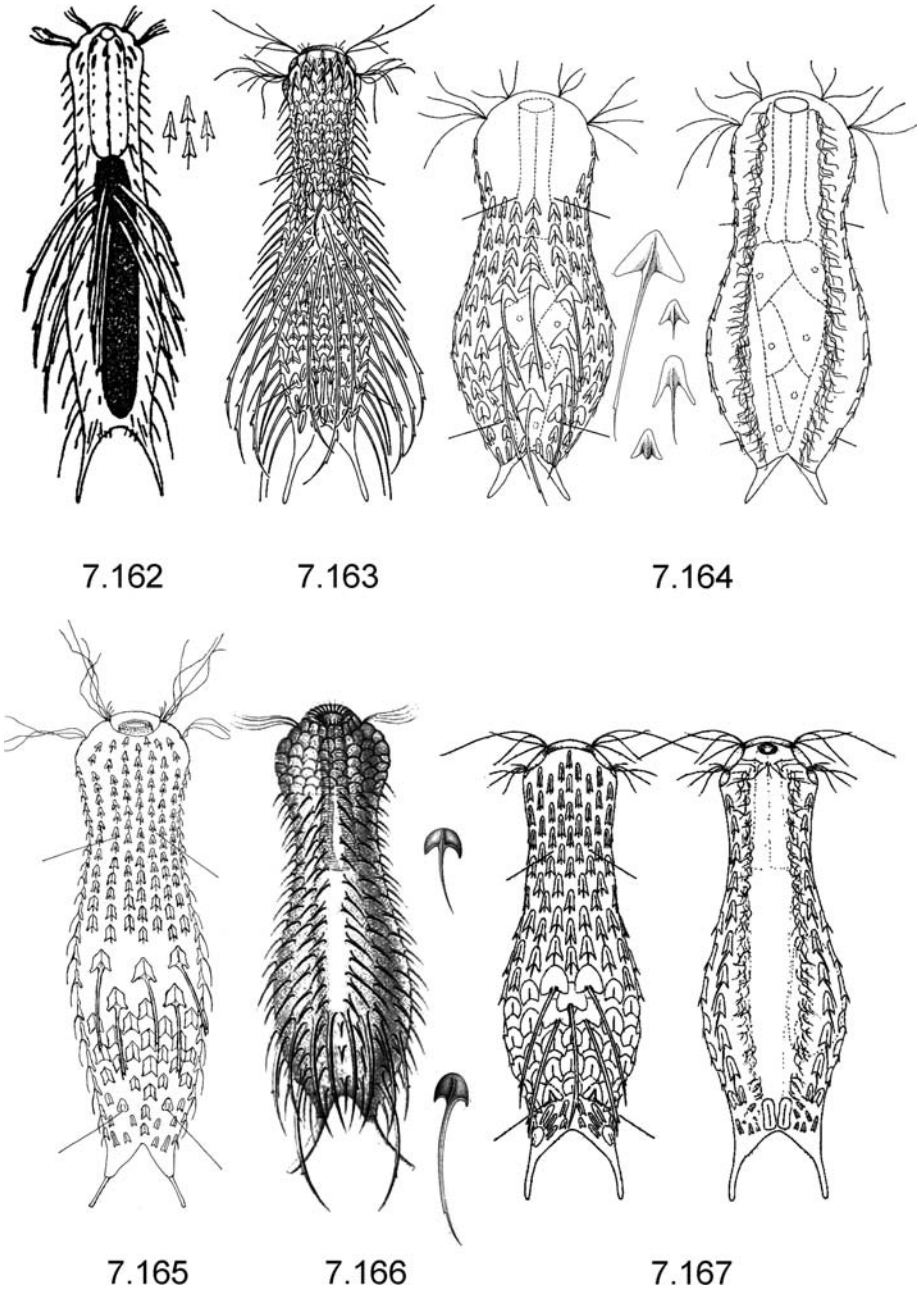


PLATE 34 Fig. 7.162 *Chaetonotus (Chaetonotus) novenarius* Greuter, 1917: dorsal view with detail of dorsal scales (modified from Greuter, 1917); Fig. 7.163 *Chaetonotus (Chaetonotus) balsamoae* Kisielewski, 1998: dorsal view (from Balsamo, 1983 with permission); Fig. 7.164 *Chaetonotus (Chaetonotus) aemilianus* Balsamo, 1978: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.165 *Chaetonotus (Chaetonotus) ferrarius* Schwank, 1990: dorsal view (from Schwank, 1990 with permission); Fig. 7.166 *Chaetonotus (Chaetonotus) heterochaetus* Daday, 1905: dorsal view with details of dorsal scales; Fig. 7.167 *Chaetonotus (Chaetonotus) pungens* Balsamo, 1990: dorsal and ventral views (from Balsamo, 1990 with permission).

62(61) Seven or eight dorsal long, thick, barbed spines arranged in a loose group; basal scales large and rounded posteriorly concave 63

62′ Five dorsal long, thick, barbed spines forming a close group on the dorsal mid trunk; basal scales large and hemi-elliptical (Fig. 7.167) ..... *Chaetonotus pungens* Balsamo, 1990
[Italy]

63(62) Seven or eight dorsal long barbed spines arranged into two columns or three series; keeled or spined scales present on the whole body 64

63′ Eight dorsal long barbed spines arranged into three columns; body cuticle bare except for very few elongate keeled scales on the dorsal posterior trunk (Fig. 7.168) ..... *Chaetonotus octonarius* Stokes, 1887
[Widespread]

64(63) Four paired long barbed spines arranged in two columns on the dorsal trunk; spined scales on the whole body (Fig. 7.169) ..... *Chaetonotus paucisetosus* Marcolongo, 1910
[Italy]

64′ Seven long, barbed spines arranged in three series on the dorsal trunk; keeled scales on the whole body (Fig. 7.170) ..... *Chaetonotus schlitzensis* Schwank, 1990
[Germany]

65(39) Dorsal spines relatively long, increasing in length caudally; scales trilobate, hemi-elliptical, hastate, or polygonal posteriorly concave, close each to the other or partially overlapping 66

65′ Dorsal spines short, simple, slightly increasing in length caudally (3–9 μm); scales trilobate with large anterior lobe and very short posterior lobes, well-spaced out (Fig. 7.171) ..... *Chaetonotus italicus* Balsamo & Todaro, 1995
[Italy]

66(65) Dorsal spines very thick, slightly bent, with concave apex 67

66′ Dorsal spines normal or thin, bent, with convex apex 69

67(65) Dorsal spines barbed, without a middle swelling, clearly bent at the insertion of the accessory point; scales polygonal posteriorly concave 68

67′ Dorsal spines with a distinct swelling in the middle piece; trilobate scales; three paired parafurcal spines, the posteriormost slightly longer than furca (Fig. 7.172) ..... *Chaetonotus bifidispinosus* Tretjakova, 1991
[Russia]

68(67) Dorsal scales pentagonal; dorsal posterior trunk covered with three series of keeled scales with no spine (Fig. 7.173) ..... *Chaetonotus oplites* Balsamo, Fregni, & Tongiorgi, 1994
[Italy]

68′ Dorsal scales almost trilobate with a very broad, rounded anterior lobe and two narrow, long posterior lobes; dorsal posterior trunk covered with spined scales (Fig. 7.174) ..... *Chaetonotus parafurcatus* Nesteruk, 1991
[Poland]

69(66) Dorsal anterior scales keeled or with spiny process 70

69′ Dorsal anterior scales with well-developed spines 72

70(69) Dorsal anterior scales keeled; trunk scales pentagonal or hastate with three keels; 2–3 paired dorsal caudal spines thick, simple or barbed 71

70′ Dorsal anterior scales with spiny process; trunk scales hexagonal with two keels and long barbed spines; 2–4 paired dorsal caudal spines thin and barbed (Fig. 7.175) ..... *Chaetonotus hoanicus* Schwank, 1990
[Germany]

71(70) All dorsal spines simple, straight, with apex rounded; trunk scales pentagonal; two paired dorsal caudal simple spines; no parafurcal spines (Fig. 7.176) ..... *Chaetonotus illiesi* Schwank, 1990

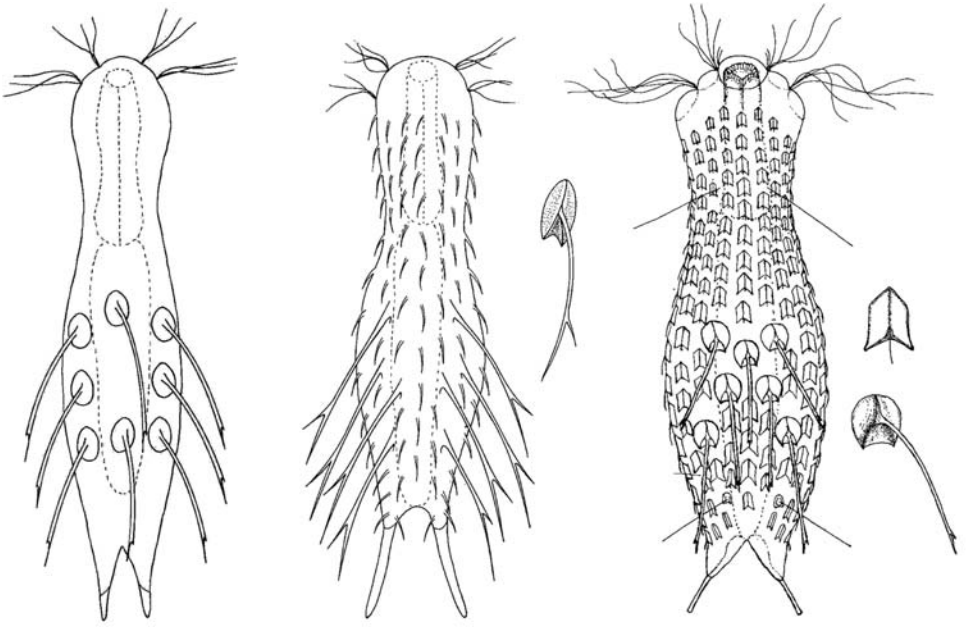
71′ Most dorsal spines barbed, slightly bent; trunk scales hastate; two paired dorsal caudal barbed spines; one paired parafurcal straight, barbed spine (Fig. 7.177) ..... *Chaetonotus heterospinosus* Balsamo, 1978
[France, Denmark, Italy, Sweden]

72(69) Dorsal trunk scales elongate, hemi-elliptical; simple spines; parafurcal spines long as furca or more 73

72′ Dorsal trunk scales hastate, cordate, polygonal, or trilobate with large anterior lobe; simple or barbed spines; parafurcal spines, if present, shorter than furca 74

73(72) Cephalic lateral plates small; seven dorsal intrafurcal spines shorter than furca; one paired, very long, thick parafurcal spine longer than furca; trunk scales hemi-elliptical, very elongate (Fig. 7.178) ..... *Chaetonotus hirsutus* Marcolongo, 1910
[Italy, Poland]

73′ Cephalic lateral plates strongly developed; nine dorsal intrafurcal spines as long as furca; no thick parafurcal spine; trunk scales hemi-elliptical (Fig. 7.179) ..... *Chaetonotus laroides* Marcolongo, 1910
[Denmark, Germany, Italy, Romania, Sweden]



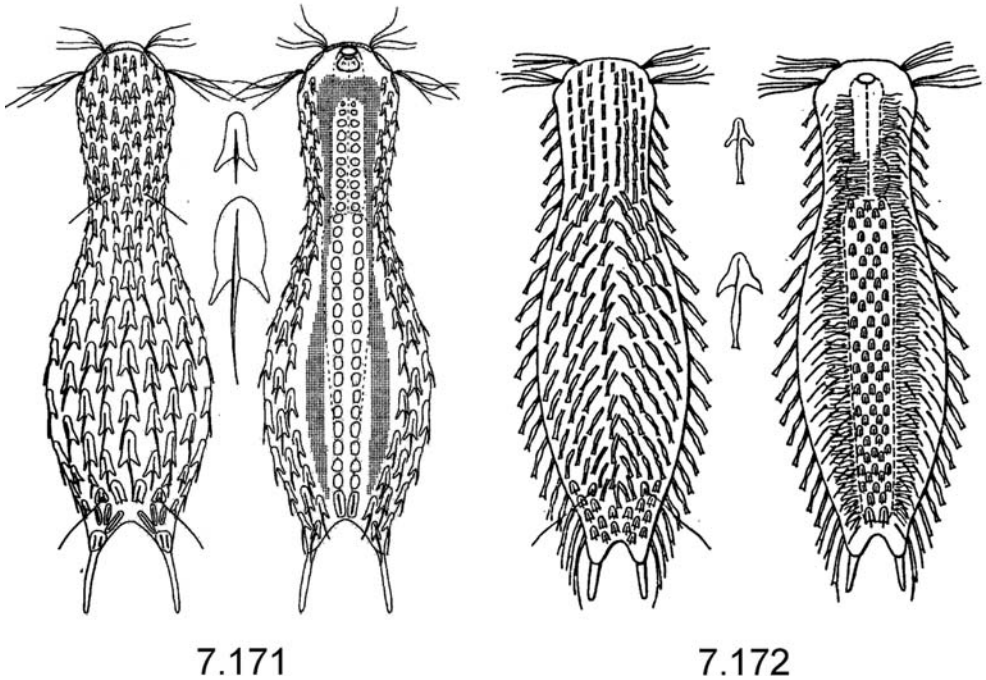
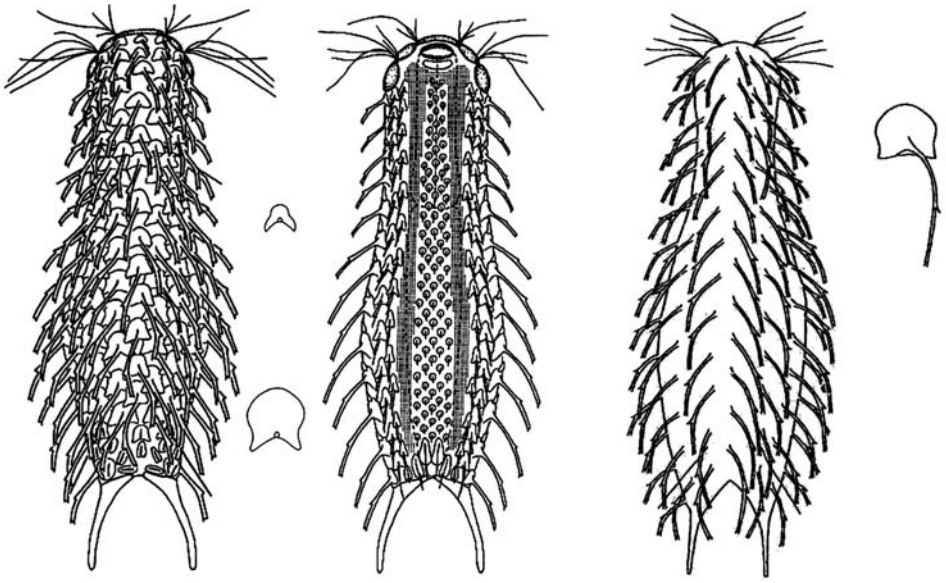
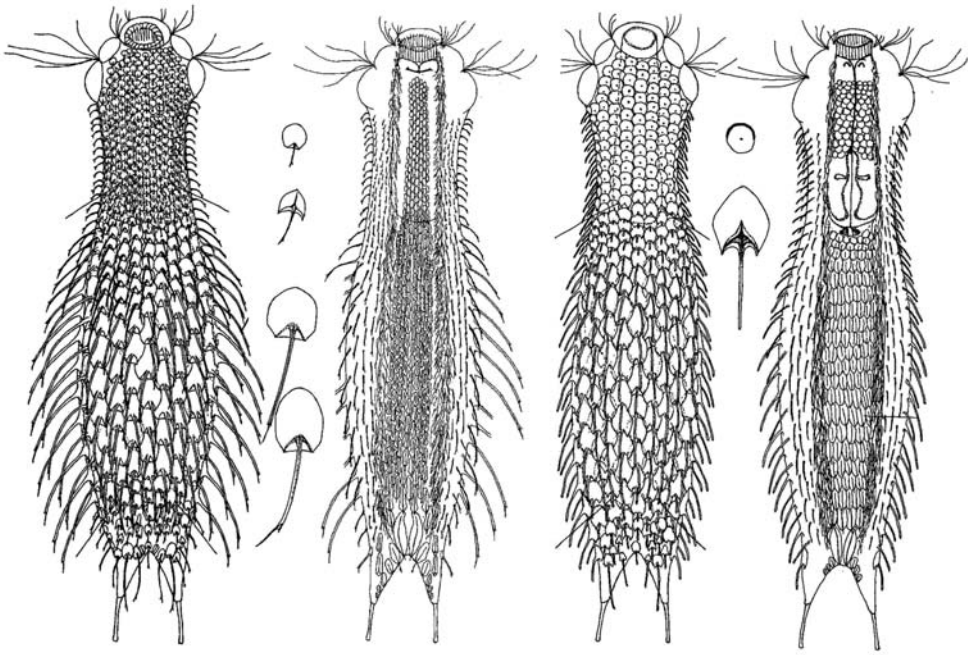


PLATE 35 Fig. 7.168 *Chaetonotus (Chaetonotus) octonarius* Stokes, 1887: dorsal view (from Balsamo, 1983 with permission); Fig. 7.169 *Chaetonotus (Chaetonotus) paucisetosus* Marcolongo, 1910: dorsal view with detail of a dorsal scale (from Balsamo, 1983 with permission); Fig. 7.170 *Chaetonotus (Chaetonotus) schlitzensis* Schwank, 1990: dorsal view with details of dorsal scales (modified from Schwank, 1990); Fig. 7.171 *Chaetonotus (Chaetonotus) italicus* Balsamo & Todaro, 1995: dorsal and ventral views with details of dorsal scales (from Balsamo & Todaro, 1995 with permission); Fig. 7.172 *Chaetonotus (Chaetonotus) bifidispinosus* Tretjakova, 1991: dorsal and ventral views with detail of dorsal scales (modified from Tretjakova, 1991).



7.173 7.174



7.175 7.176

PLATE 36 Fig. 7.173 *Chaetonotus (Chaetonotus) oplites* Balsamo, Fregni, & Tongiorgi, 1994: dorsal and ventral views with details of dorsal scales (from Balsamo, Fregni, & Tongiorgi, 1994 with permission); Fig. 7.174 *Chaetonotus (Chaetonotus) parafurcatus* Nesteruk, 1991: dorsal view with detail of dorsal scales (from Nesteruk, 1991 with permission); Fig. 7.175 *Chaetonotus (Chaetonotus) hoanicus* Schwank, 1990: dorsal and ventral views with details of dorsal scales (modified from Schwank, 1990); Fig. 7.176 *Chaetonotus (Chaetonotus) illiesi* Schwank, 1990: dorsal and ventral views with details of dorsal scales (from Schwank, 1990 with permission).

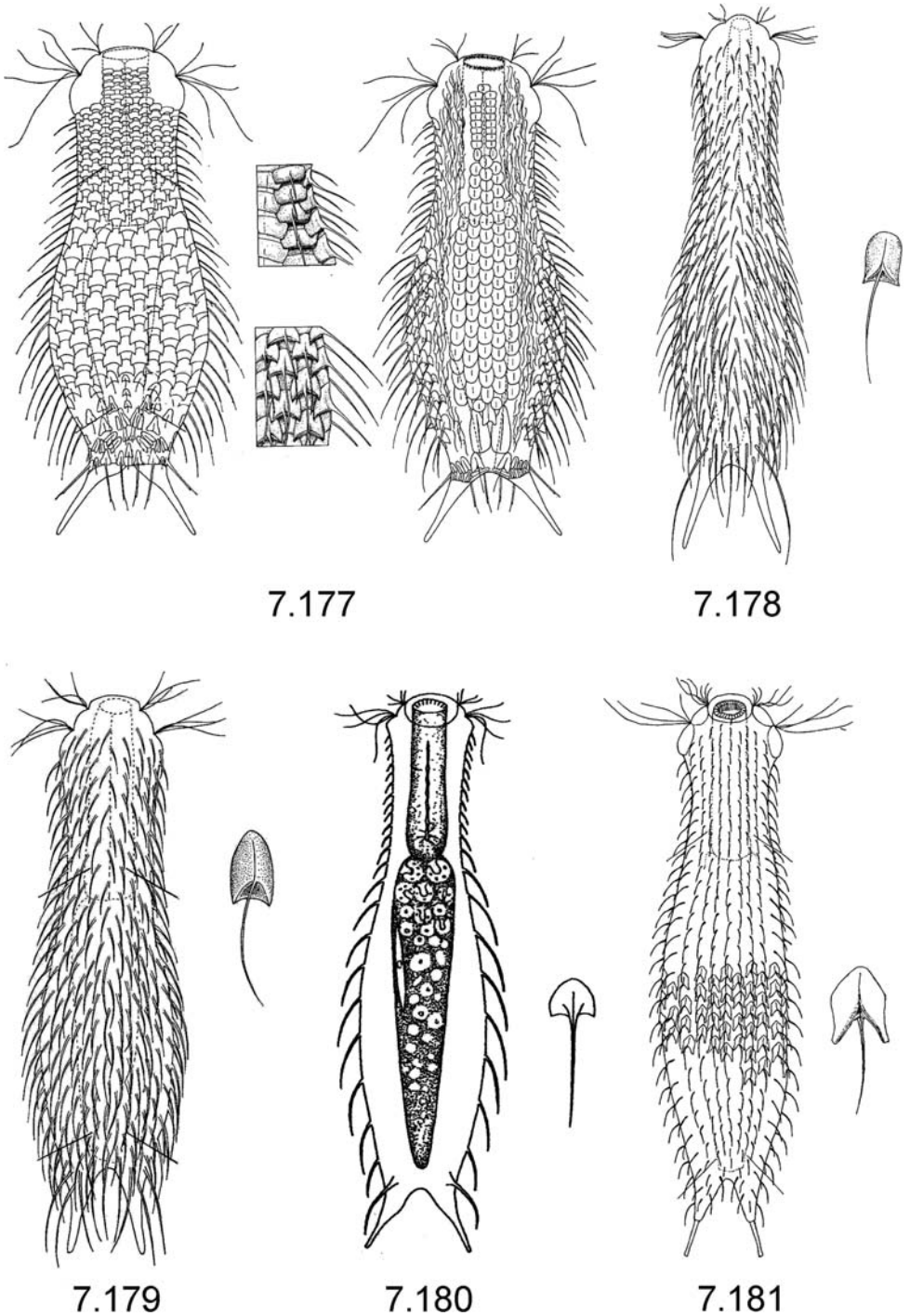


PLATE 37 Fig. 7.177 *Chaetonotus (Chaetonotus) heterospinosus* Balsamo, 1978: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.178 *Chaetonotus (Chaetonotus) hirsutus* Marcolongo, 1910: dorsal view with detail of a dorsal scale (from Balsamo, 1983 with permission); Fig. 7.179 *Chaetonotus (Chaetonotus) laroides* Marcolongo, 1910: dorsal view with detail of a dorsal scale (from Balsamo, 1983 with permission); Fig. 7.180 *Chaetonotus (Chaetonotus) rarispinosus* Roszczak, 1935: dorsal view with detail of a dorsal scale (from Roszczak, 1969 with permission); Fig. 7.181 *Chaetonotus (Chaetonotus) pratensis* Schwank, 1990: dorsal view with detail of a dorsal scale (modified from Schwank, 1990).

74(72) Dorsal spines simple 75

74′ Dorsal spines barbed, at least on the trunk 77

75(74) One or two paired parafurcal spines slightly bent; dorsal scales not hastate, deeply concave posteriorly; 3−5 dorsal caudal spines 76

75′ One paired thick parafurcal spine strongly bent; dorsal trunk scales hastate slightly concave posteriorly; no dorsal caudal spines (Fig. 7.180) ..... *Chaetonotus rarispinosus* Roszczak, 1935
[Poland]

76(75) Dorsal trunk scales pentagonal; one paired short parafurcal spine (Fig. 7.181) ..... *Chaetonotus pratensis* Schwank, 1990
[Germany]

76′ Dorsal trunk scales hastate; three paired parafurcal spines (Fig. 7.182) ..... *Chaetonotus maximus* Ehrenberg, 1830
[Widespread]

77(74) All dorsal spines barbed; trunk spines long up to twice the anterior ones 78

77′ Dorsal anterior spines simple, trunk spines barbed and long, up to 4−5 times the anterior ones; all spines quite upright from the body cuticle; three unpaired short dorsal caudal spines (Fig. 7.183) ..... *Chaetonotus remanei* Schwank, 1990
[Germany]

78(77) Dorsal scales not pentagonal 79

78′ Dorsal scales pentagonal and anteriorly pointed; dorsal spines of similar length (Fig. 7.184) ..... *Chaetonotus dybowskii* Jakubski, 1919
[Poland, Romania, Ukraine]

79(78) Posterior trunk covered with spined scales; dorsal scales unkeeled 80

79′ Dorsal posterior trunk covered with 3−4 series of small keeled scales; dorsal scales hastate and keeled (Fig. 7.185) ..... *Chaetonotus similis* Zelinka, 1889
[Widespread]

80(79) Dorsal scales cordate; three paired dorsal caudal spines, the medial protruding in the intrafurcal space (Fig. 7.186) ..... *Chaetonotus longisetosus* Preobrajenskaia, 1926
[Romania, Russia]

80′ Dorsal scales trilobate with large anterior lobe and long, narrow posterior lobes; no dorsal caudal intrafurcal spines (Fig. 7.187) ..... *Chaetonotus alni* Nesteruk, 1991
[Poland]

Gastrotricha: Chaetonotida: Chaetonotidae: *Lepidodermella* Species

1 Scales with anterior double edge, partially overlapping 2

1′ Scales with simple edge, juxtaposed 6

2(1) One or two paired long parafurcal spines 3

2′ No parafurcal spines 4

3(2) One paired, short (<10 µm) parafurcal spine; ventral field with few caudal scales; one lateral cuticular tooth in the mouth cavity (Fig. 7.188) ..... *Lepidodermella intermedia* Kånneby, Todaro & Jondelius, 2012
[Denmark, Sweden]

3′ Two paired long (>20 µm) parafurcal spines; ventral field wholly scaled; no tooth in the mouth cavity (Fig. 7.189) ..... *Lepidodermella spinifera* Tretjakova, 1991
[Russia]

4(2) Pharynx of normal length (1/3 body length) without teeth; ventral field wholly covered with smooth scales 5

4′ Pharynx very short (1/5 body length) with 1−2 anterior teeth; few ventral terminal scales (Fig. 7.190) ..... *Lepidodermella minor* (Remane, 1936)
[Germany, Poland, Sweden]

5(4) One paired strong spined scale on the dorsal furca base (Fig. 7.191) ..... *Lepidodermella acantholepida* Suzuki & Furuya, 2013
[Japan]

5′ No spined scales on the dorsal furca base (Fig. 7.192) ..... *Lepidodermella squamata* Dujardin, 1841
[Widespread. Afrotropical, Australian, Nearctic, Neotropical, Oriental]

6(1) Head as wide as the trunk or less; more than nine dorsal columns of scales 7

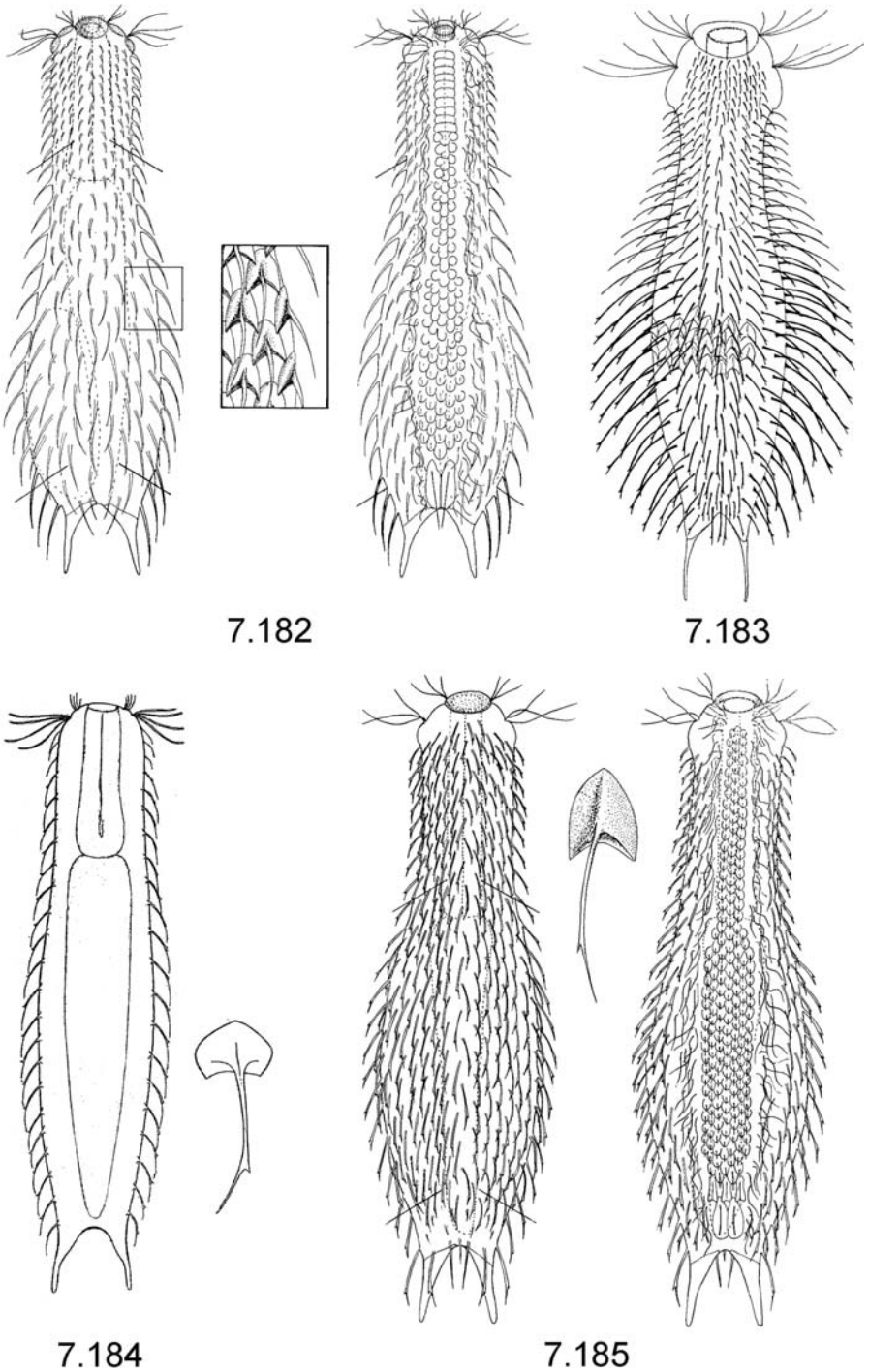
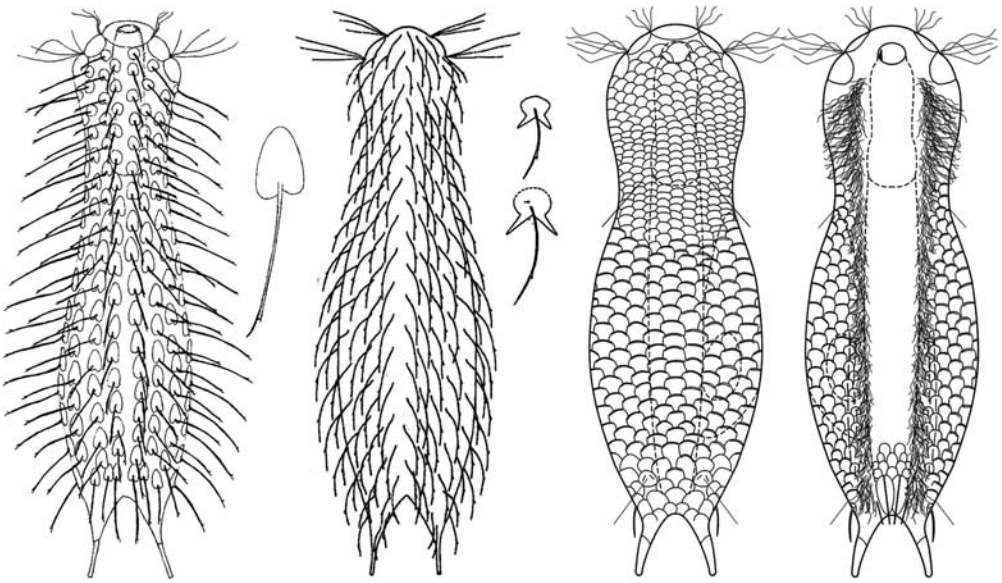
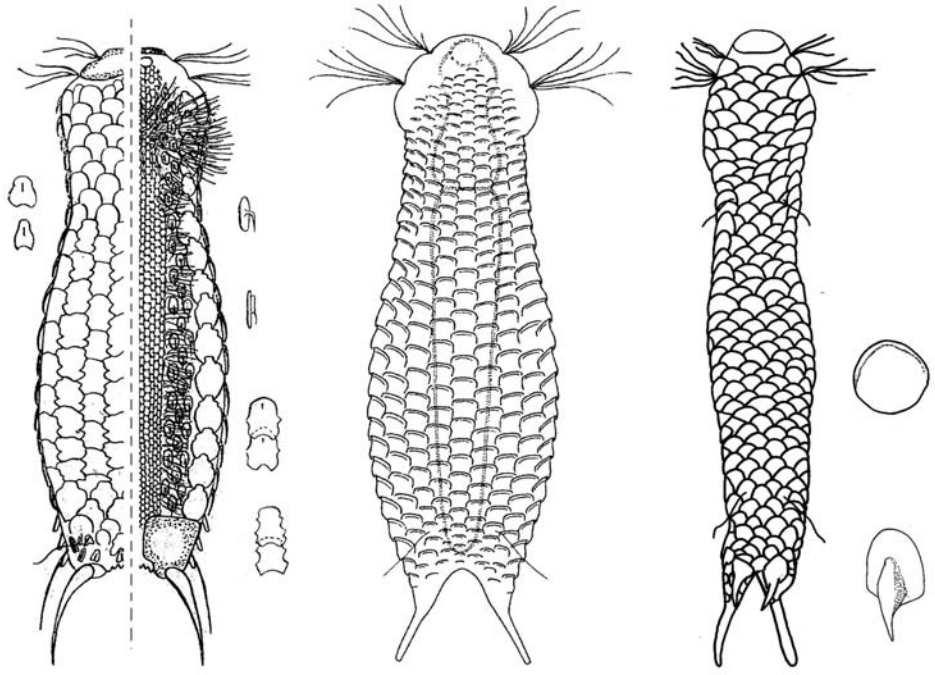


PLATE 38 Fig. 7.182 *Chaetonotus (Chaetonotus) maximus* Ehrenberg, 1830: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.183 *Chaetonotus (Chaetonotus) remanei* Schwank, 1990: dorsal view (modified from Schwank, 1990); Fig. 7.184 *Chaetonotus (Chaetonotus) dybowskii* Jakubski, 1919: dorsal view with detail of a dorsal scale (from Roszczak, 1969, with permission); Fig. 7.185 *Chaetonotus (Chaetonotus) similis* Zelinka, 1889: dorsal and ventral views with detail of a dorsal scale (from Balsamo, 1983 with permission).



7.186 7.187 7.188



7.189 7.190 7.191

PLATE 39 Fig. 7.186 *Chaetonotus (Chaetonotus) longisetosus* Preobrajenskaia, 1926: dorsal view with detail of a dorsal scale (redrawn from Preobrajenskaia, 1926); Fig. 7.187 *Chaetonotus (Chaetonotus) alni* Nesteruk, 1991: dorsal view with detail of dorsal scales (from Nesteruk, 1991 with permission); Fig. 7.188 *Lepidodermella intermedia* Kånneby, Todaro & Jondelius, 2012: dorsal and ventral views (from Kånneby, Todaro, & Jondelius, 2012 with permission); Fig. 7.189 *Lepidodermella spinifera* Tretjakova, 1991: schematic composition of dorsal view (*left*) and ventral view (*right*) with details of dorsal scales (modified from Tretjakova, 1991); Fig. 7.190 *Lepidodermella minor* (Remane, 1936): dorsal view (from Kisielewski, 1998 with permission).; Fig. 7.191 *Lepidodermella acantholepida* Suzuki & Furuya, 2013: dorsal view with details of dorsal scales (modified from Suzuki et al., 2013).

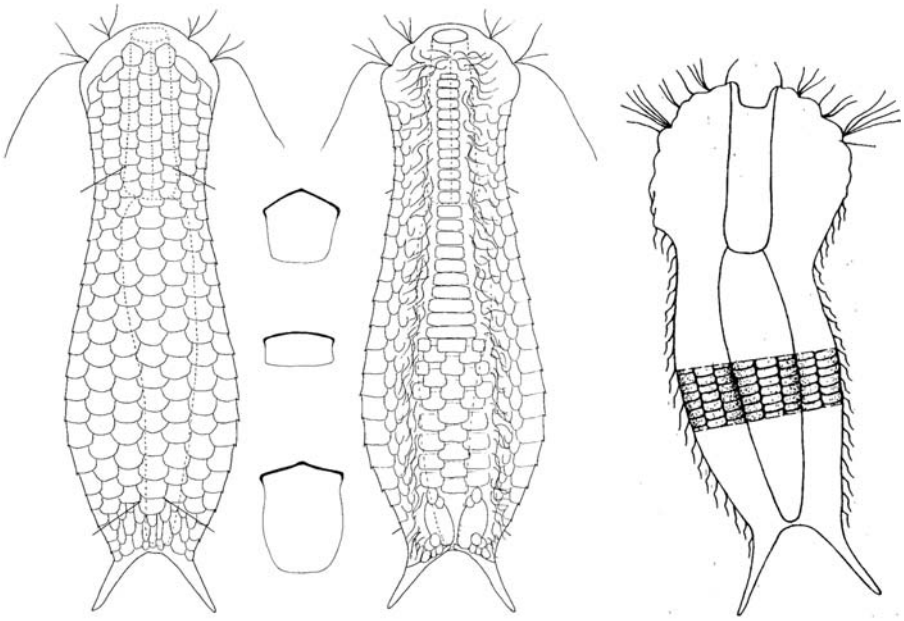
6′	Head much wider than the trunk; nine dorsal columns of hexagonal scales (Fig. 7.193) ..... *Lepidodermella macrocephala* d'Hondt, 1972 [France]
7(6)	Ventral field wholly scaled or bare; ≤15 dorsal columns of scales 8
7′	Ventral field with few caudal plates; 15−20 dorsal columns of 70−80 scales (Fig. 7.194) ..... *Lepidodermella serrata* Sudzuki, 1971 [Japan]
8(7)	Hexagonal scales 9
8′	Rounded scales; ventral field with numerous keels and two terminal thin keeled scales (Fig. 7.195) ..... *Lepidodermella zelinkai* Konsuloff, 1913 [Bulgaria, Germany, Poland, Romania, United Kingdom]
9(8)	Furca base without scales; adhesive tubes long 2/3 furca length; ventral field bare (Fig. 7.196) ..... *Lepidodermella aspidioformis* Sudzuki, 1971 [Japan]
9′	Furca base scaled; adhesive tubes very short (1/4 furca length) (Fig. 7.197) ..... *Lepidodermella tabulata* Preobrajenskaia, 1926 [Romania, Russia]

Gastrotricha: Chaetonotida: Chaetonotidae: *Fluxiderma*: Species

1	Dorsal scales papilliform or circular, arranged into numerous columns covering the whole body; large furca base 2
1′	Few dorsal plates flat and smooth arranged into four columns on the neck and trunk; narrow furca base (Fig. 7.198) ..... *Fluxiderma montanum* Rudescu, 1967 [Romania]
2(1)	Fifteen dorsal columns of >50 very small, papilliform scales also covering the furca base (Fig. 7.199) ..... *Fluxiderma concinnum* (Stokes, 1887) [Italy. Nearctic]
2′	Nine dorsal columns of 25−28 circular scales not covering the furca base (Fig. 7.200) ..... *Fluxiderma verrucosum* (Roszczak, 1936) [Poland]

Gastrotricha: Chaetonotida: Chaetonotidae: *Aspidiophorus*: Species

1	Long, straight, simple paired spines arising on the caudal body end 2
1′	No spines on the caudal body end 7
2(1)	Few to several dorsal and lateral paired caudal spines 3
2′	Numerous (>10) dorsal, lateral, and ventral paired caudal spines, straight and as long as furca (Fig. 7.202) ..... *Aspidiophorus pori* Kisielewski, 1999 [Israel]
3(2)	Few (<5) dorsal straight paired caudal spines 4
3′	Several dorsal and lateral, slightly bent paired caudal spines (Fig. 7.203) ..... *Aspidiophorus aster* Martin, 1981 [United Kingdom]
4(3)	One or three dorsolateral paired caudal spines; rhomboidal scales 5
4′	Two paired dorsal caudal spines; rounded scales (Fig. 7.204) ..... *Aspidiophorus tetrachaetus* Kisielewski, 1986 [Poland, Russia, Sweden]
5(4)	One dorsolateral and three median paired caudal spines 6
5′	Three dorsolateral paired caudal spines; no median caudal spines (Fig. 7.205) ..... *Aspidiophorus squamulosus* Roszczak, 1936 [Denmark, Italy, Poland, Sweden]
6(5)	Dorsolateral caudal spines long twice as furca; scales unkeeled (Fig. 7.206) ..... *Aspidiophorus longichaetus* Kisielewski, 1986 [Poland]
6′	Dorsolateral caudal spines shorter than furca; scales with three keels (Fig. 7.207) ..... *Aspidiophorus heterodermus* Saito, 1937 [Israel, Italy, Japan]
7(1)	Scales rhomboidal 8
7′	Scales not rhomboidal 12



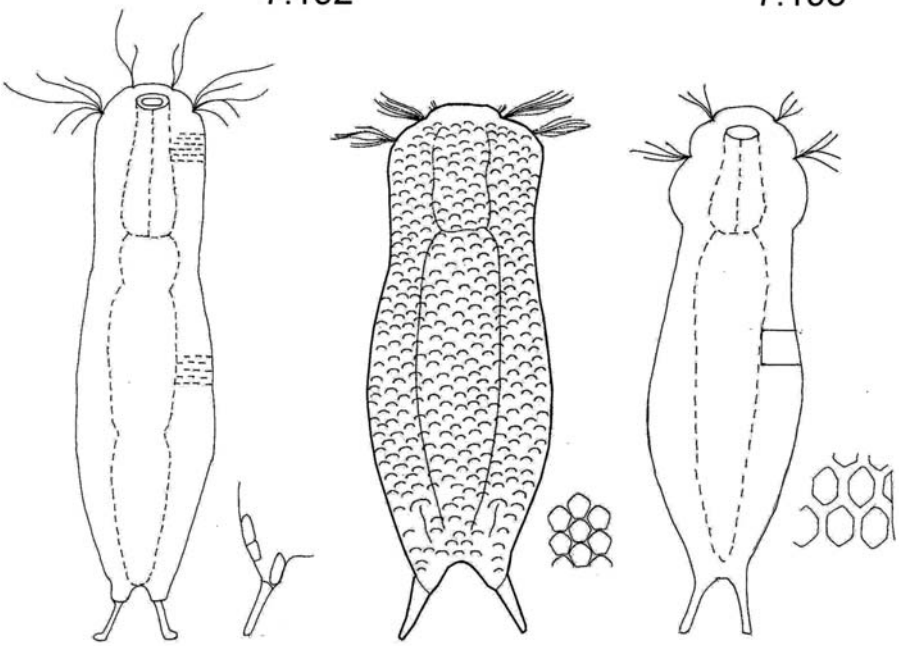


PLATE 40 Fig. 7.192 *Lepidodermella squamata* Dujardin, 1841: dorsal and ventral views with details of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.193 *Lepidodermella macrocephala* d'Hondt, 1972: dorsal view with a detail of the dorsal scales (modified from d'Hondt, 1972); Fig. 7.194 *Lepidodermella serrata* Sudzuki, 1971: dorsal view with a detail of the caudal furca (modified from Sudzuki, 1971); Fig. 7.195 *Lepidodermella zelinkai* Konsuloff, 1913: dorsal view with detail of dorsal scales (from Konsuloff, 1913); Fig. 7.196 *Lepidodermella aspidioformis* Sudzuki, 1971: dorsal view with a detail of dorsal scales (modified from Sudzuki, 1971).

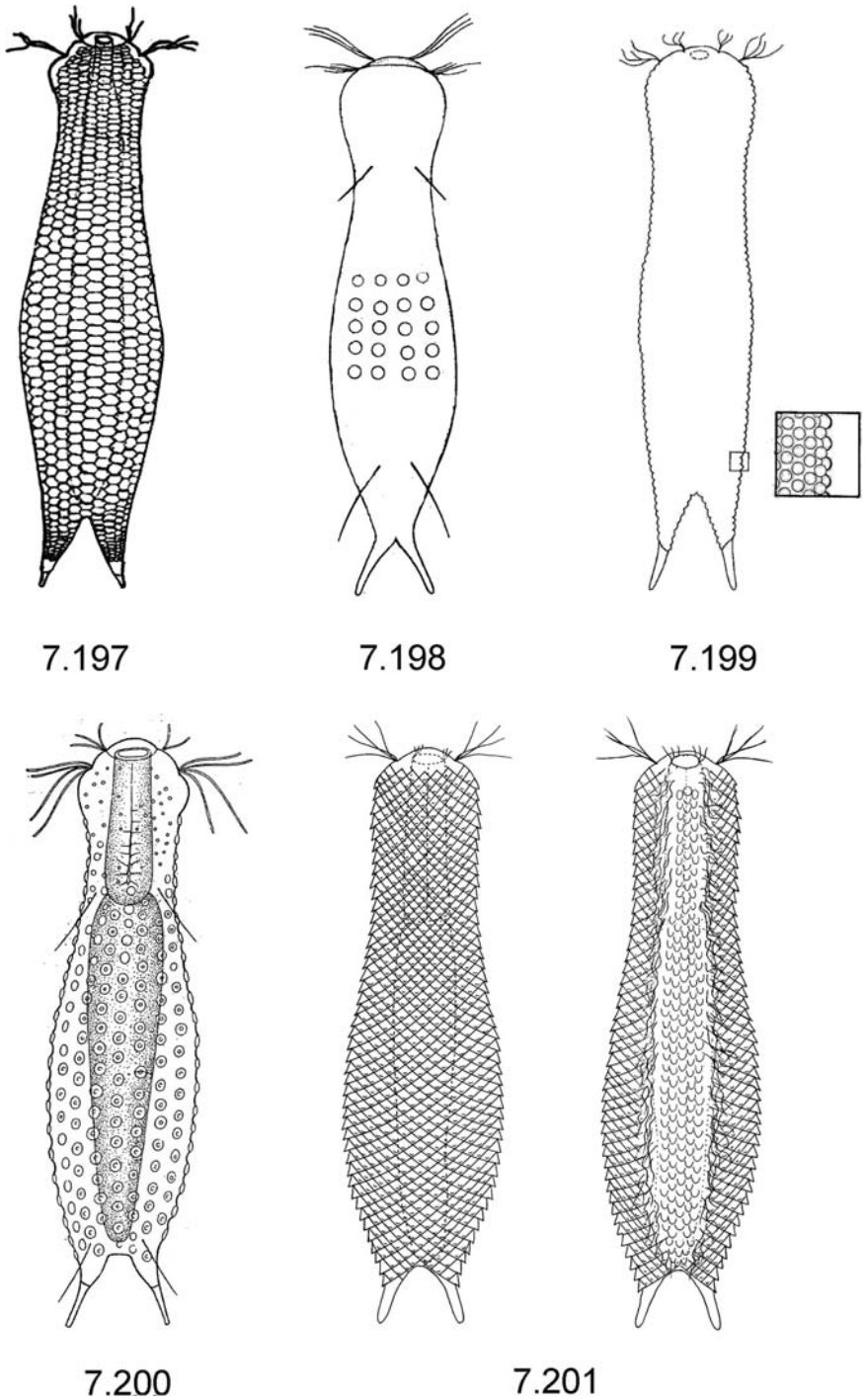


PLATE 41 Fig. 7.197 *Lepidodermella tabulata* Preobrajenskaia, 1926: dorsal view (modified from Preobrajenskaia, 1926); Fig. 7.198 *Fluxiderma montanum* Rudescu, 1967: dorsal view (modified from Rudescu, 1967); Fig. 7.199 *Fluxiderma concinnum* (Stokes, 1887): dorsal view with a detail of the cuticular ornamentation (from Balsamo, 1983 with permission); Fig. 7.200 *Fluxiderma verrucosum* (Roszczak, 1936): dorsal view (from Roszczak, 1969 with permission); Fig. 7.201 *Rhomballichtys punctatus* (Greuter, 1917): dorsal and ventral views (from Balsamo, 1983 with permission).

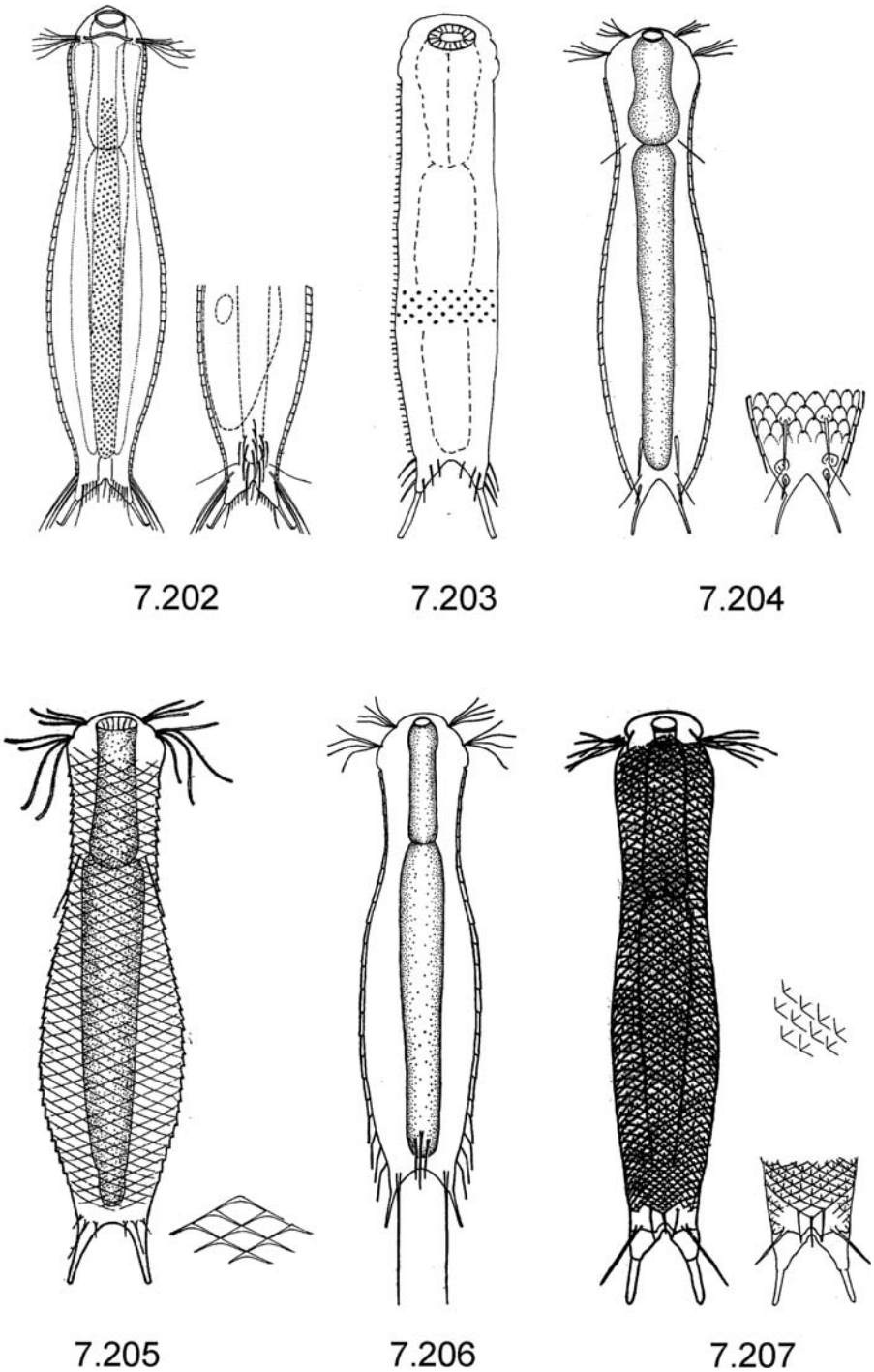


PLATE 42 Fig. 7.202 *Aspidiophorus pori* Kisielewski, 1999: dorsal view with a detail of the ventral posterior end (from Kisielewski, 1999 with permission); Fig. 7.203 *Aspidiophorus aster* Martin, 1981: schematic dorsal view with a detail of dorsal scales (redrawn from Martin, 1981); Fig. 7.204 *Aspidiophorus tetrachaetus* Kisielewski, 1986: dorsal view with a detail of the dorsal posterior end (from Kisielewski, 1986 with permission); Fig. 7.205 *Aspidiophorus squamulosus* Roszczak, 1936: dorsal view with a detail of the dorsal scales (from Roszczak, 1969 with permission); Fig. 7.206 *Aspidiophorus longichaetus* Kisielewski, 1986: dorsal view (from Kisielewski, 1986 with permission); Fig. 7.27 *Aspidiophorus heterodermus* Saito, 1937: dorsal view with details of the dorsal scales and of the dorsal posterior end.

8(7) Furca short or very short; scales without a median keel 9

8′ Furca normally developed; scales with a median keel 11

9(8) Large body size (>150 µm); adhesive tubes pointed; no ocelli 10

9′ Medium body size (<135 µm); adhesive tubes thick, broadened at the tip; two small ocelli (Fig. 7.208) ..... *Aspidiophorus oculifer* Kisielewski, 1981
[Germany, Italy, Poland, Russia, Sweden. Neotropics]

10(9) Trilobate head; ventral field bare (Fig. 7.209) ..... *Aspidiophorus nipponensis* Schwank, 1990
[Japan]

10′ Pentalobate head; ventral field caudally scaled (Fig. 7.210) ..... *Aspidiophorus polonicus* Kisielewski, 1981
[Germany, Poland]

11(8) Dorsal surface with 25 columns of 40−45 distinct scales (Fig. 7.211) ..... *Aspidiophorus paradoxus* Voigt, 1902
[Widespread]

11′ Dorsal surface with 50 columns of 120 extremely small scales ..... *Aspidiophorus microlepidotus* d'Hondt, 1978
[France]

12(7) Scales rounded 13

12′ Scales elongate or indistinct 14

13(12) Small body size (<100 µm); furca base bare; no intrapharyngeal cuticular structures (Fig. 7.212) ..... *Aspidiophorus semirotundus* Saito, 1937
[Japan]

13′ Medium body size (>150 µm), furca base scaled; intrapharyngeal cuticular structures (Fig. 7.213) ..... *Aspidiophorus slovinensis* Kisielewski, 1986
[Poland, Russia]

14(12) Elongate scales with spiny process 15

14′ Extremely small scales hardly visible 16

15(14) Keeled scales arranged into 41−44 dorsal columns (Fig. 7.214) ..... *Aspidiophorus ophiodermus* Balsamo, 1983
[Italy, Poland, Russia, Sweden, United Kingdom. Neotropics]

15′ Unkeeled scales arranged into 25−30 dorsal columns (Fig. 7.215) ..... *Aspidiophorus schlitzensis* Schwank, 1990
[Germany]

16(14) Large body size (>170 µm); narrow cylindrical pharynx 17

16′ Medium body size (<150 µm); pharynx with two marked bulbs (Fig. 7.216) ..... *Aspidiophorus bibulbosus* Kisielewski, 1979
[Israel, Poland, Russia]

17(16) Neck region slightly swollen; scales peduncles extremely short (Fig. 7.217) ..... *Aspidiophorus microsquamatus* Saito, 1937
[Japan, Poland]

17′ Neck region cylindrical; scales peduncles well developed, appearing as spines (Fig. 7.218) ..... *Aspidiophorus tatraensis* Kisielewski, 1986
[Poland]

Gastrotricha: Chaetonotida: Chaetonotidae: *Heterolepidoderma*: Species

1 Slender body with very elongate, cylindrical trunk; large body size (>130 µm); keeled scales arranged in parallel columns and juxtaposed 2

1′ Fusiform body with rounded, short trunk; small body size (75−120 µm); scales generally keeled, arranged in parallel and/or converging columns, and generally overlapping 6

2(1) Furca normal or short, with adhesive tubes not pointed; no clear constriction at the furca base 3

2′ Furca very long, with bare base and long, pointed adhesive tubes; clear body constriction at the furca base; oval scales (Fig. 7.219) ..... *Heterolepidoderma longicaudatum* Kisielewski, 1979
[Poland]

3(2) Furca with adhesive tubes of normal length; <50 columns of dorsal scales; no spines on the intrafurcal edge 4

3′ Furca with adhesive tubes very short (~1/4 furca length) with tip weakly bifurcated; >50 columns of scales poorly visible; one paired short spine on the intrafurcal edge (Fig. 7.220) ..... *Heterolepidoderma brevitubulatum* Kisielewski, 1981
[Poland]

4(3) Very elongate, elliptical scales clearly keeled; no ocelli 5

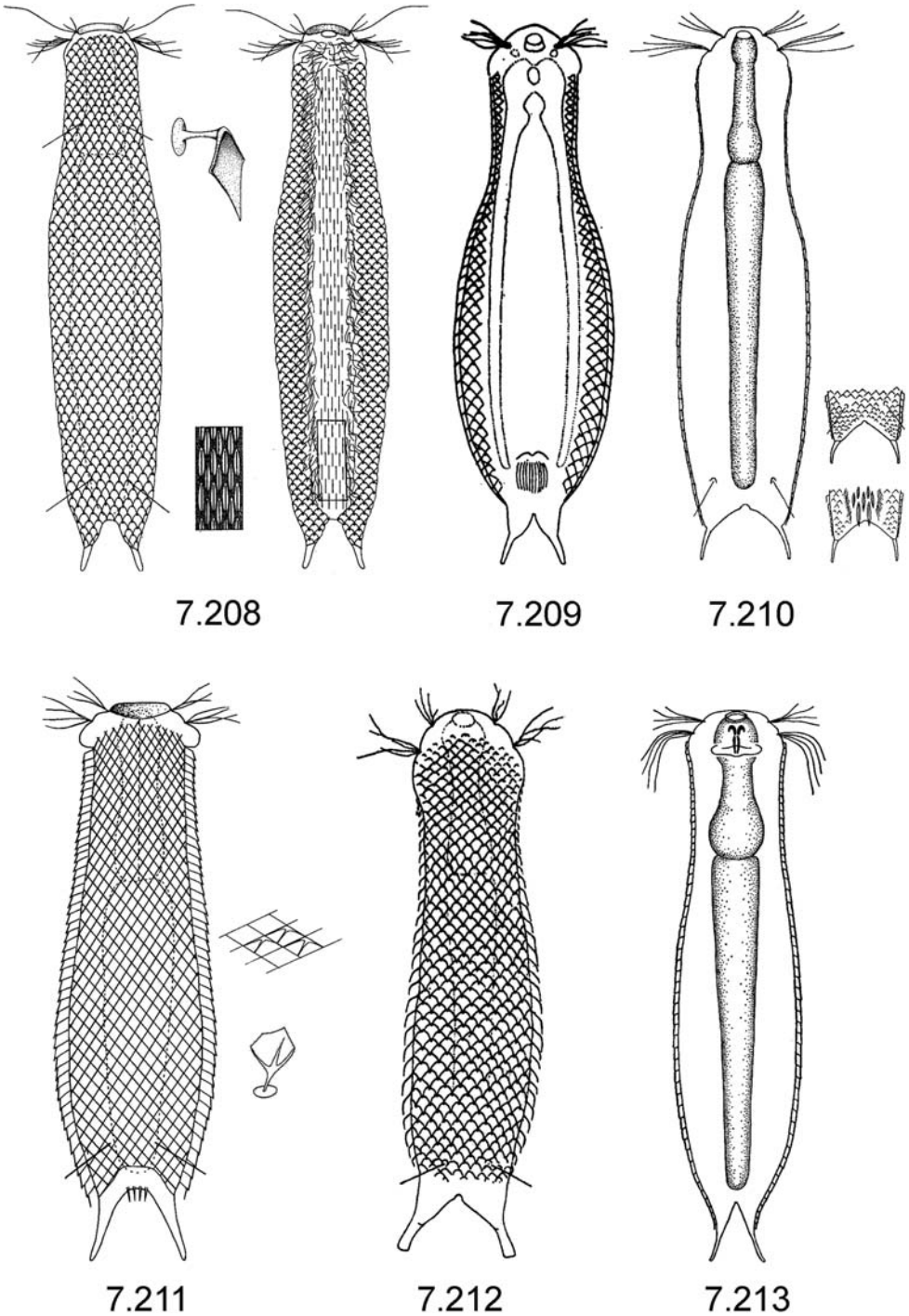
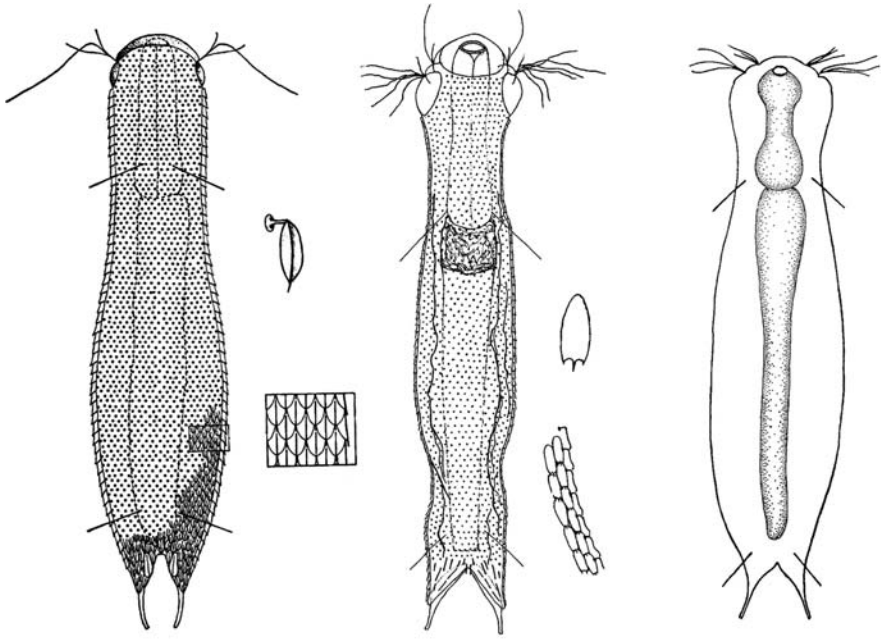
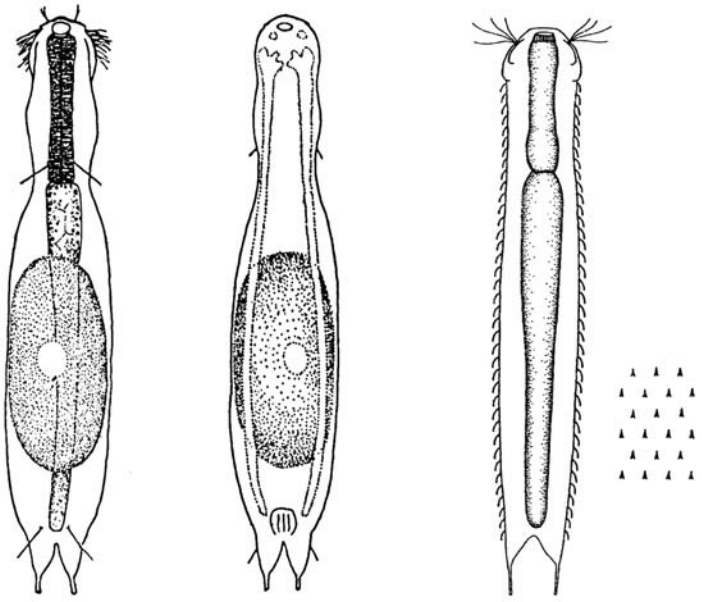


PLATE 43 Fig. 7.208 *Aspidiophorus oculifer* Kisielewski, 1981: dorsal and ventral views with details of a dorsal scale and ventral interciliary scales (from Balsamo, 1990 with permission); Fig. 7.209 *Aspidiophorus nipponensis* Schwank, 1990: ventral view (modified from Saito, 1937); Fig. 7.210 *Aspidiophorus polonicus* Kisielewski, 1981: schematic dorsal view with details of the dorsal and ventral posterior ends (modified from Kisielewski, 1981); Fig. 7.211 *Aspidiophorus paradoxus* (Voigt, 1902): dorsal view with details of dorsal scales and a single dorsal scale (from Balsamo, 1983 with permission); Fig. 7.212 *Aspidiophorus semirotundus* Saito, 1937: dorsal view (modified from Saito, 1937); Fig. 7.213 *Aspidiophorus slovinensis* Kisielewski, 1986: schematic dorsal view (from Kisielewski, 1986 with permission).



7.214 7.215 7.216



7.217 7.218

PLATE 44 Fig. 7.214 *Aspidiophorus ophiodermus* Balsamo, 1983: dorsal view with details of dorsal scales and a single dorsal scale (from Balsamo, 1983 with permission); Fig. 7.215 *Aspidiophorus schlitzensis* Schwank, 1990: dorsal view with details of dorsal scales and a single dorsal scale (modified from Schwank, 1990); Fig. 7.216 *Aspidiophorus bibulbosus* Kisielewski, 1979: dorsal view (from Kisielewski, 1979 with permission); Fig. 7.217 *Aspidiophorus microsquamatus* Saito, 1937: dorsal and ventral views (modified from Saito, 1937); Fig. 7.218 *Aspidiophorus tatraënsis* Kisielewski, 1986: dorsal view with a detail of cuticular ornamentation (from Kisielewski, 1986 with permission).

4′ Small, hexagonal scales faintly keeled; two small ocelli (Fig. 7.221) ..... *Heterolepidoderma gracile* Remane, 1927
[Germany, Israel, Japan, Poland, Romania, Russia]

5(4) Trilobate head with strongly developed kephalion, epipleuria, and hypostomion; 25 dorsal columns of scales (Fig. 7.222) ..... *Heterolepidoderma majus* Remane, 1927
[Germany, Japan, Poland, Romania (?)]

5′ Pentalobate head with small cephalic plates; 35–40 dorsal columns of scales (Fig. 7.223) ..... *Heterolepidoderma kossinense* (Preobrajenskaia, 1926)
[Romania, Russia]

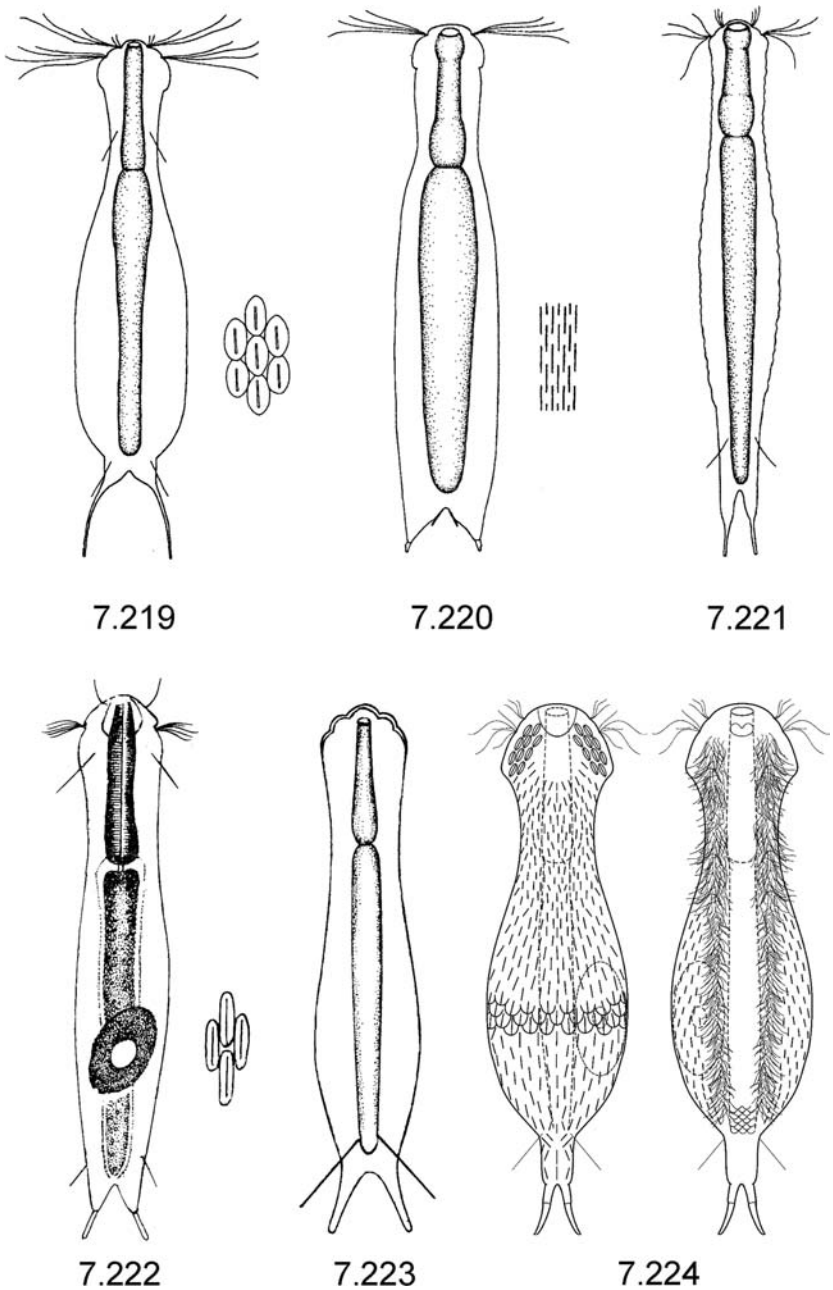


PLATE 45 Fig. 7.219 *Heterolepidoderma longicaudatum* Kisielewski, 1979: dorsal view with a detail of dorsal scales (from Kisielewski, 1979 with permission); Fig. 7.220 *Heterolepidoderma brevitubulatum* Kisielewski, 1981: dorsal view with a detail of dorsal scales (modified from Kisielewski, 1981); Fig. 7.221 *Heterolepidoderma gracile* Remane, 1927: dorsal view (modified from Remane, 1927); Fig. 7.222 *Heterolepidoderma majus* Remane, 1927: dorsal view with detail of dorsal scales (modified from Remane, 1927); Fig. 7.223 *Heterolepidoderma kossinense* (Preobrajenskaia, 1926): dorsal view (modified from Preobrajenskaia, 1926); Fig. 7.224 *Heterolepidoderma trapezoidum* Kånneby, 2011: dorsal and ventral views (from Kånneby, 2011 with permission).

6(1) Caudal trunk region gradually narrowing; dorsal scales uniformly present 7

6′ Caudal trunk region extremely narrowed; dorsal scales lacking on the central head surface (Fig. 7.224) ..... *Heterolepidoderma trapezoidum* Kånneby, 2011 [Sweden]

7(6) Pharynx with two bulbs; rod-like or granular cuticular structures into the anterior bulb 8

7′ Pharynx cylindrical or with one posterior bulb; no intrapharyngeal cuticular structures 10

8(7) Furca base scaled; two bacilliform intrapharyngeal structures 9

8′ Furca base bare; four bacilliform and two granular intrapharyngeal structures (Fig. 7.225) ..... *Heterolepidoderma dimentmani* Kisielewski, 1999 [Israel]

9(8) Scales of the ventrolateral medial columns provided with a lamellar expansion; 13−17 dorsal columns of scales; no dorsal large scale on the furca base (Fig. 7.226) ..... *Heterolepidoderma lamellatum* Balsamo & Fregni, 1995 [Italy]

9′ Scales of the ventrolateral medial columns without a lamellar expansion; 21−23 dorsal columns of scales; one paired dorsal large scale on the furca base (Fig. 7.227) ..... *Heterolepidoderma joermungandri* Kånneby, 2011 [Sweden]

10(7) ≥40 dorsal columns of scales 11

10' ≤27 dorsal columns of scales 13

11(10) Dorsal scales extremely small, hardly visible 12

11′ Dorsal scales elliptical, keeled, with spiny process (Fig. 7.228) ..... *Heterolepidoderma multiseriatum* Balsamo, 1978 [Italy]

12(11) Three paired long keeled scales and one unpaired median keeled scale with spiny process on the dorsal furca base (Fig. 7.229) ..... *Heterolepidoderma tenuisquamatum* Kisielewski, 1981 [Germany, Poland]

12′ No scales on the dorsal furca base (Fig. 7.230) ..... *Heterolepidoderma obesum* d'Hondt, 1967 [France]

13(10) Dorsal scales with spiny process 14

13′ Dorsal scales without spiny process 16

14(13) Dorsal scales elliptical; furca base scaled 15

14′ Dorsal scales subtriangular with no apparent keel; furca base bare (Fig. 7.231) ..... *Heterolepidoderma pineisquamatum* Balsamo, 1981 [Italy, Germany]

15(14) A series of 3−8 long simple spines on the dorsal trunk; often ventrolateral spines (Fig. 7.232) ..... *Heterolepidoderma acidophilum* Kånneby, Todaro, & Jondelius, 2012 [Poland, Russia, Sweden]

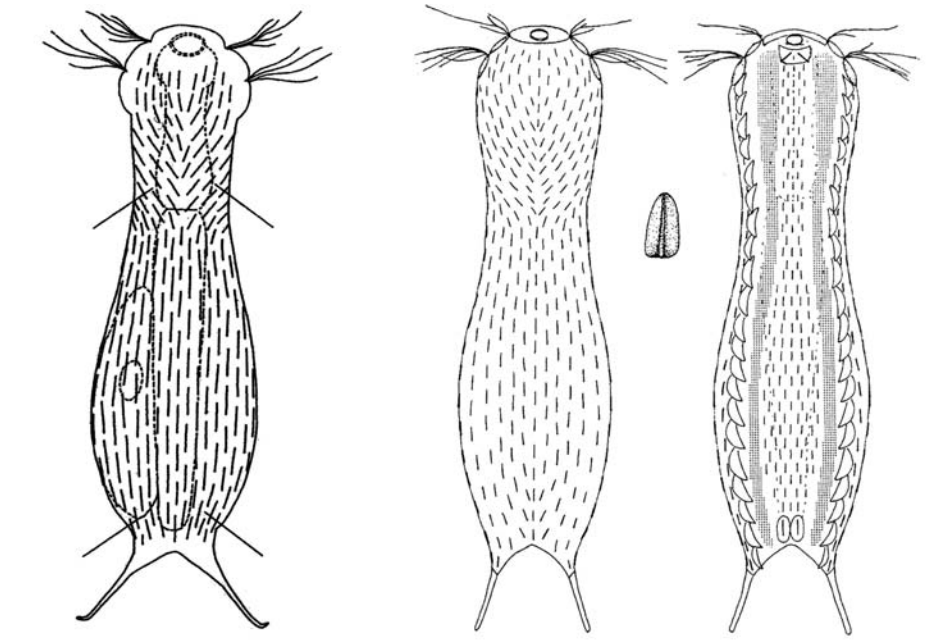
15′ No dorsal or ventrolateral spines (Fig. 7.233) ..... *Heterolepidoderma ocellatum* (Metschnikoff, 1865) [Widespread. Nearctic, Neotropics]

16(13) Keeled scales elliptical, clearly distinct, arranged irregularly or in parallel columns converging on the caudal trunk 17

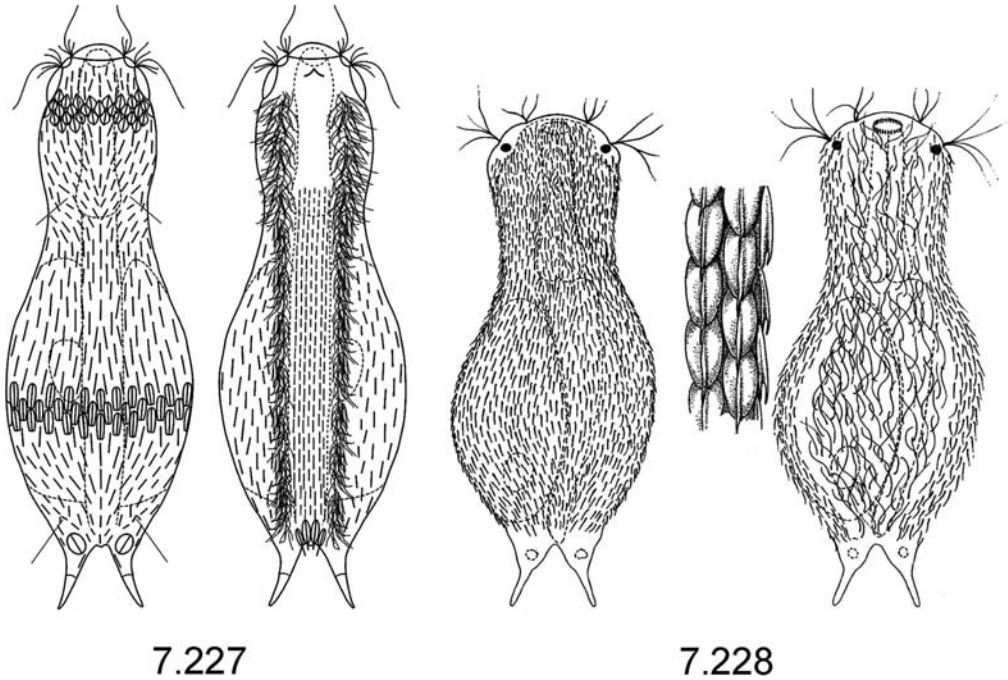
16′ Keeled scales with edges hardly visible; dorsal scales arranged in parallel columns converging on the neck and on the caudal trunk (Fig. 7.234) ..... *Heterolepidoderma macrops* Kisielewski, 1981 [France, Germany, Japan (?), Poland, Sweden, Russia. Nearctic (?)]

17(16) Large keeled scales irregularly arranged on the trunk; furca base scaled (Fig. 7.235) ..... *Heterolepidoderma patella* Schwank, 1990 [Germany]

17′ Thin keeled scales arranged in parallel columns converging on the posterior trunk, furca base bare (Fig. 7.236) ..... *Heterolepidoderma obliquum* Saito, 1937 [Japan]

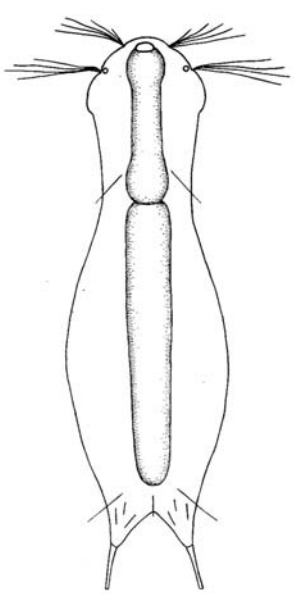


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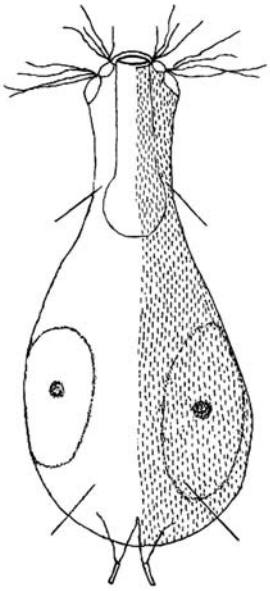


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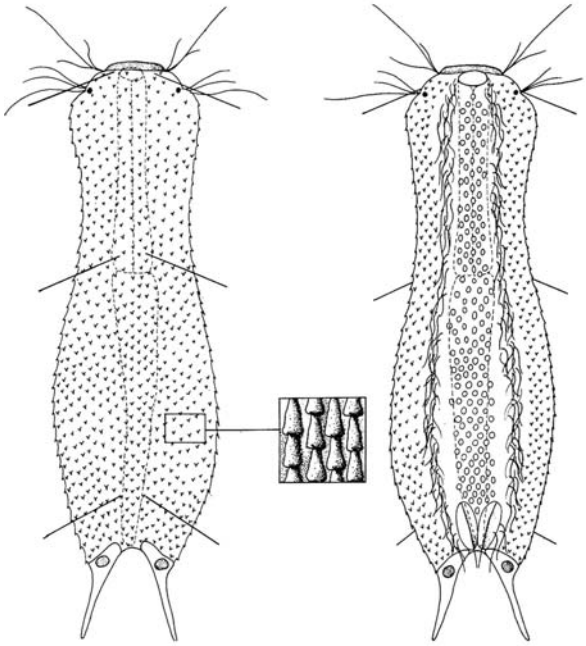
PLATE 46 Fig. 7.225 *Heterolepidoderma dimentmani* Kisielewski, 1999: dorsal view (from Kisielewski, 1999 with permission); Fig. 7.226 *Heterolepidoderma lamellatum* Balsamo & Fregni, 1995: dorsal and ventral views with a detail of a dorsal scale (from Balsamo & Fregni, 1995 with permission); Fig. 7.227 *Heterolepidoderma joermungandri* Kånneby, 2011: dorsal and ventral views (from Kånneby, 2011 with permission); Fig. 7.228 *Heterolepidoderma multiseriatum* Balsamo, 1978: dorsal and ventral views with a detail of dorsal scales (from Balsamo, 1983 with permission).



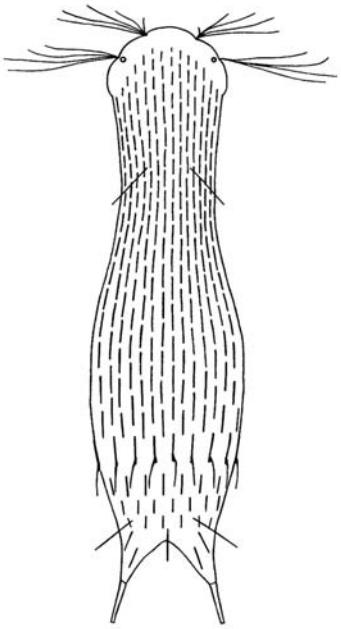
7.229



7.230



7.231



7.232

PLATE 47 Fig. 7.229 *Heterolepidoderma tenuisquamatum* Kisielewski, 1981: dorsal view (modified from Kisielewski, 1981); Fig. 7.230 *Heterolepidoderma obesum* d'Hondt, 1967: dorsal view: dorsal scaling is represented on the right body side (modified from Schwank, 1990); Fig. 7.231 *Heterolepidoderma pineisquamatum* Balsamo, 1981: dorsal and ventral views with a detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.232 *Heterolepidoderma acidophilum* Kånneby, Todaro, & Jondelius, 2012: dorsal view (modified from Kisielewski, 1981).

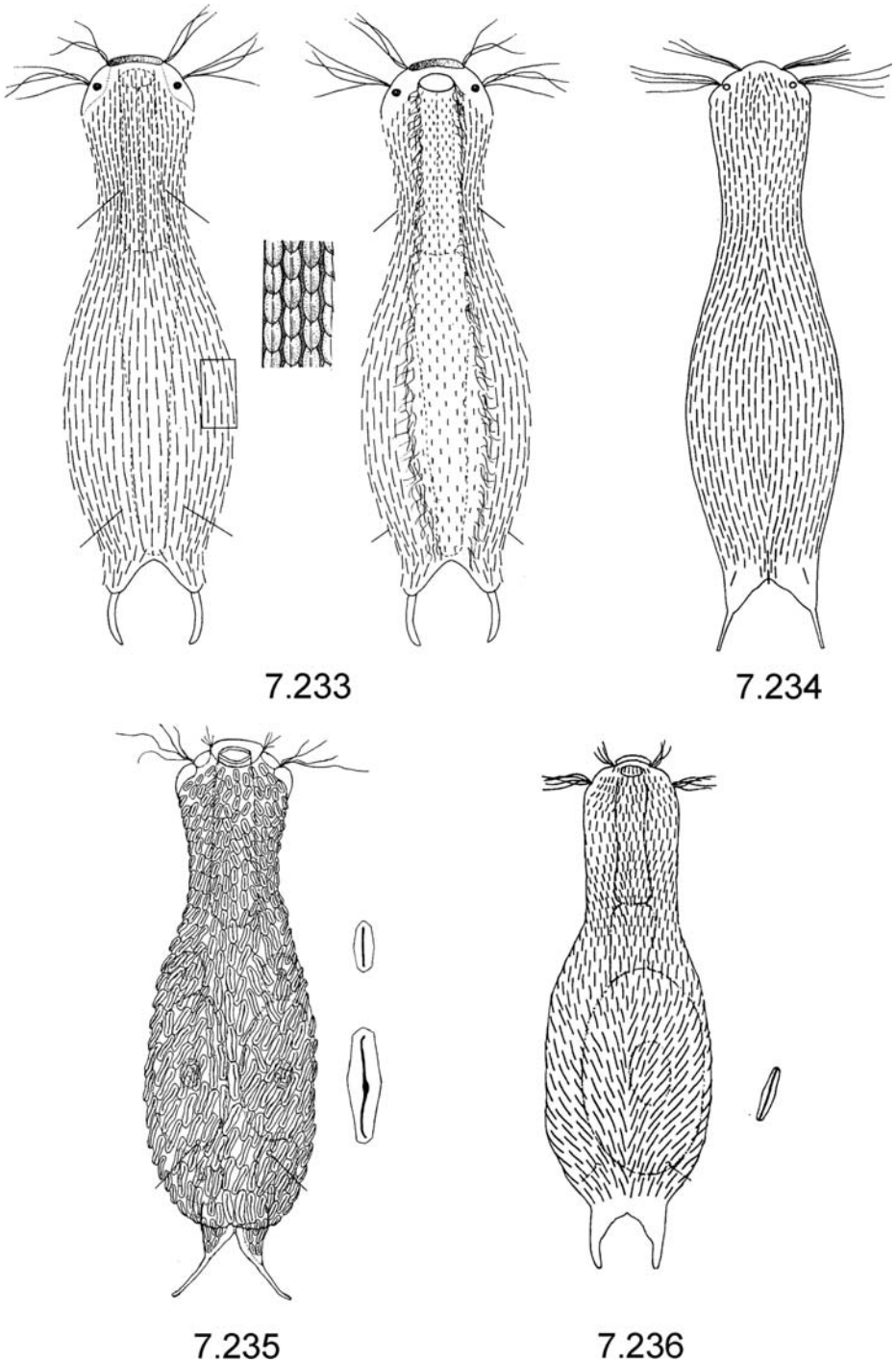


PLATE 48 Fig. 7.233 *Heterolepidoderma ocellatum* (Metschnikoff, 1865): dorsal and ventral views with a detail of dorsal scales (from Balsamo, 1983 with permission); Fig. 7.234 *Heterolepidoderma macrops* Kisielewski, 1981: dorsal view (modified from Kisielewski, 1981); Fig. 7.235 *Heterolepidoderma patella* Schwank, 1990: dorsal view with a detail of dorsal scales (from Schwank, 1990 with permission); Fig. 7.236 *Heterolepidoderma obliquum* Saito, 1937: dorsal view with a detail of a dorsal scale (modified from Saito, 1937).

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Chapter 8

Phylum Rotifera

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INTRODUCTION

Classification schemes differ slightly in how they regard the four rotifer groups: Seisonidea, Bdelloidea, Monogononta, and Acanthocephala, the latter being an obligatorily parasitic taxon previously treated as a distinct phylum (Garey et al., 1996; Garey et al., 1998; Mark Welch &

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Meselson, 2000; Fontaneto & Jondelius, 2011; Sielaff et al., 2016). The peculiar problem is that outside of the phylogenetic literature, acanthocephalans and rotifers are still treated separately. Basically, each group of taxonomists has ignored much of the research done by the other. However, as evidenced in the works cited above, there is ample support to unite the two taxa within a single classification. First, they both share an important, unique, synapomorphic characteristic: within the syncytial integument of both lies a curious layer of two proteins called the intracytoplasmic lamina. These proteins provide a degree of stiffness to the body wall depending on its thickness. More importantly, molecular evidence supports uniting these taxa; indeed researchers are now arguing that acanthocephalans ought to be subsumed within Rotifera (Sørensen & Giribet, 2006; Segers, 2007; Wey-Fabrizius et al., 2014). Thus a new classification is emerging, one which asserts that acanthocephalans and seisonids are sister groups within Pararotatoria (Min & Park 2009; Fontaneto & Jondelius, 2011; Wey-Fabrizius et al., 2014; Sielaff et al., 2016). Pararotatoria + bdelloids then comprise Hemirotifera, with Hemirotifera and Monogononta comprising the Syndermata (Witek et al., 2008). Syndermata is then a sister taxon to the Gnathostomulida, thus creating a group of small, jawed animals, the Gnathifera (Sørensen, 2001; Leasi et al., 2012). The close affinity among these taxa has led some to propose that the Gnathifera be treated as a distinct phylum (Shiel et al., 2009). However, given the scope of this work, we ignore the problem of where to place the acanthocephalans and gnathostomulids, but look forward to additional study that will provide a better synthesis of these taxa.

At one time, rotifers were divided into two classes: those with two gonads (seisonids and bdelloids) were considered to be orders within class Digononta, leaving the Monogononta as a separate class (Pennak, 1989). In this key, two classes, Pararotatoria and Eurotatoria, are recognized (Melone & Ricci, 1995; Smith, 2001; Segers, 2002; Wallace et al., 2006; Wallace & Smith, 2009; Wallace & Snell, 2010). Older classification systems that consider rotifers as a class within the Phylum Aschelminthes should be abandoned.

Systematics of Rotifer Classes

Class Pararotatoria, Subclass Seisonidea

This taxon is comprised of only two genera (*Paraseison* and *Seison*), each with two species. These are large (2–3 mm) dioecious, marine rotifers that live on the gills of crustaceans (Ricci, 1993; Sørensen et al., 2005; Leasi et al., 2011, 2012). Sometimes described as aberrant, the corona of seisonids is very reduced and not used in locomotion. All species have paired gonads and a functional gut in both sexes. The jaws or trophi are described as being fulcrate. Females have ovaries without vitellaria. Sexes are of similar size and morphology. This family is not covered herein.

Class Eurotatoria, Subclass Bdelloidea

This important subclass is comprised of 19 genera and, depending on the author, approximately nearly 500 species (Ricci, 1987; Segers, 2002, 2007, 2008). A complicating factor in determining an accurate estimation of the number of species is that cryptic species seem to be widespread in bdelloids (Fontaneto et al., 2007a, 2009, 2011). Bdelloids possess a somewhat uniform body plan (Donner, 1965; Melone & Ricci, 1995) and are exclusively females, reproducing by parthenogenesis. Bdelloids are characterized by having paired ovaries with vitellaria, more than two pedal glands, and ramate trophi (Melone et al,. 1998; Wallace & Ricci, 2002; Wallace & Snell, 2010). Nearly all bdelloids are microphagous with a corona of either two trochal discs or a modified ciliated field. Bdelloids often have a vermiform body with a pseudo-segmentation consisting of annuli that permits shortening and lengthening of the body by telescoping. Current taxonomy recognizes three orders: Adinetida (Adinetidae), Philodinida (Habrotrochidae and Philodinidae), and Philodinavida (Philodinavidae) (Melone & Ricci, 1995).

Bdelloids generally are not caught in plankton tows, although they may be found in waters with dense vegetation. On the other hand, they often occur in sediments or among plant debris or crawling on the surfaces of aquatic plants. Some forms inhabit the capillary water films of soils (Pourriot, 1979; Devetter, 2010) or covering mosses (Burger, 1948; Peters et al., 1993; Ricci & Caprioli, 2005; Bielańska-Grajner et al., 2011); this habitat has been referred to as the limnoterrestrial (Devetter, 2008; Segers, 2008). Bdelloids also are present in communities that develop in tree holes (Devetter, 2008) and the pitfall traps of the carnivorous plant *Sarracenia purpurea* Linnaeus, 1753 (Bateman, 1987; Błedzki & Ellison, 1998). Many species are capable of becoming desiccated and then rehydrated (Ricci & Fontaneto, 2009; Wilson, 2011). Unfortunately, there has been no systematic review of bdelloids, but there are several works that should be consulted for more information (Bartoš, 1951; Donner, 1965; Pourriot, 1979; Koste & Shiel, 1986; Melone et al., 1998; Ricci & Melone, 2000).

Class Eurotatoria, Subclass Monogononta

The monogononts comprise the largest group of rotifers, with >1500 species in more than 100 genera. While most are free living with a benthic, free-swimming, or sessile existence, a few genera are parasitic. Nearly all rotifers are found in inland waters, both fresh and alkaline, but some

appear to be exclusive to the marine habitat. In many species, males have never been observed, but all monogononts are assumed to be dioecious. As the name implies, these rotifers possess a single gonad. Males are often structurally reduced with a vestigial gut that functions only in energy storage (Ricci & Melone, 1998). They have a shorter lifespan than females and are usually present in the plankton for only a few days or weeks each year. Monogononts are microphagous or raptorial, but a few are parasitic. The corona is more varied than in other rotifers; the corona may range from broad to narrow disks or possess auriciform lobes or be fusiform with reduced ciliation and long setae that are used in prey capture. This key recognizes two superorders: Pseudotrocha (order Ploima) and Gnesiotrocha (orders Collothecaceae and Flosculariaceae).

LIMITATIONS

Here we recognize 34 rotiferan families (four bdelloid and 30 monogononts) with >130 genera. Of these, ~110 genera and ~900 species, have been reported from inland waters of the Palearctic. Regardless of the extensive taxonomic work done in the Palearctic, we feel that this assessment is an underestimation of the true species richness. [In this work we have attempted to update the estimated number of species in each genus, as well as correct typographical errors from Wallace et al. (2016). However, we note that rotifer taxonomy remains in flux so that the taxa enumerated herein are our best approximations.]

Except for the incomplete "Guide Series" (Segers, 1995a,b; De Smet, 1996; De Smet & Pourriot, 1997; Nogrady & Segers, 2002; Wallace et al., 2006), there has been no attempt to construct a comprehensive key to Rotifera. There are a variety of keys to rotifers, including those by Edmondson (1959) and Smith (2001), which cover some of the North American fauna to the level of genus, and Stemberger (1979) for the Laurentian Great Lakes, which provides a species-level key. Although specialized and covering other biogeographical realms, valuable keys can be found for Australian waters (Koste & Shiel, 1986, 1987, 1989a,b, 1990a,b, 1991; Shiel & Koste 1992, 1993; Shiel, 1995), the British Isles (Pontin, 1978), Italy (Braioni & Gelmini, 1983), and for planktonic rotifers in general (Ruttner-Kolisko, 1974). Unfortunately, no key is comprehensive enough to cover all of the variations in size and morphology that are sometimes found within a species. Of all the efforts, Koste's (1978) revision of Voigt for the rotifers of central Europe comes closest; although over 35 years old, it is still important. We urge caution in using keys that are available in electronic form (e.g., on the Internet or on CD-ROMs). In most instances these are oversimplified, often reflecting a suite of species from a rather narrow geographic region; in no way should they be considered thorough. Nevertheless, Jersabek et al. (2014) and Jersabek & Leitner (2013) are two very valuable online resources.

A further limitation stems from the fact that too few species have photographic documentation. Thus, as with other Rotifera keys, we caution that the illustrations used in this one are not necessarily from specimens collected from the Palearctic and we have had to rely on illustrations from the older literature. When the figures used to demonstrate the general form of a taxon are from the Palearctic they are designed with the abbreviation PAL. For this work we estimated the number of species in each genus using the assessment of Segers (2007) including subspecific variants (subspecies), but not those species noted as *species inquirenda*—species requiring additional investigation before being accepted as a valid taxon. We also did not count species that appear to be strict halophiles (only inhabiting marine and brackish waters), recognizing that they could still be present in alkaline, inland waters.

Finally, it should be noted that emerging molecular data support the concept of cryptic speciation in rotifers. Thus, there may be 3–14 times as many species within any currently recognized morphospecies (Gómez, 2005; Fontaneto et al., 2007a,b; Schröder & Walsh, 2007; Garcia-Morales & Elias-Gutierrez, 2013).

One of the fundamental differences among the higher taxonomic levels in the phylum Rotifera is the structure of the trophi that reside in a muscular pharynx called the mastax. Nine different types of trophi are recognized, along with various transitional forms (Koste, 1978; Koste & Shiel, 1987). Although the following key is designed with the nonspecialist in mind, commensurate with the central importance of the trophi, we use both the structure of the trophi and other obvious characters of anatomy and morphology as principal points of separation of the taxa. Therefore, it is important to note that you may have to destroy one or more specimens to get a good look at the trophi. Consequently, because other morphological features also are critical to identification, it is important that you reserve several specimens to study whole, preferably alive. Taking photomicrographs of the live, intact animal before preservation or hydrolysis is always a prudent practice.

The obligatory marine class Pararotatoria (Seisonidae) is not included herein. The following key is based on several important works (Koste, 1978; Segers, 2004; Wallace et al., 2006). The species records annotated herein for the Palearctic are noted in brackets; monospecific genera are designated as such. All data were derived from Segers (2007).

TERMINOLOGY AND MORPHOLOGY

Most rotifer **trophi** are composed of seven hardened elements or **sclerites** (Fig. 8.1; also Fig. 13.19 in Volume I).

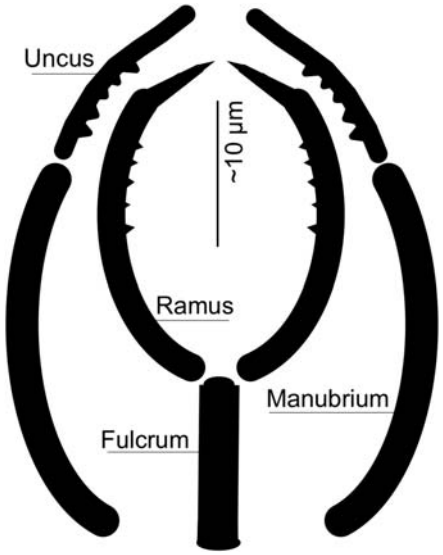


FIGURE 8.1 Schematic view of the basic elements of rotifer trophi. (See also Figs. 13.10 and 11 in Volume I for a complete overview of the trophi.)

Three of these, the **manubrium** (manubria), **ramus** (rami), and **uncus** (unci) are paired, while the **fulcrum** is unpaired (see also Fig. 13.10 in Volume I). The central-most elements are the rami that may contain one or more chambers. The fulcrum, which is absent in bdelloids, is located caudally between the rami and articulates with them. Together, the fulcrum and paired rami comprise the **incus**. Located left and right of the rami are the manubrium and uncus; together they comprise the **malleus** (plural, mallei). These elements are all held together and are moved by muscular action. Besides the discussion in Volume I of this series, additional information on rotifer trophi may be found in the following works: Donner (1956), Edmondson (1959), Koste (1978), and Sørensen (2006). The nine different types of trophi were established based on the size, shape, and positioning of the seven elements described above, as well as the presence of other accessory parts and variations. The "Rotifer trophi web page" (Anon, 2014) also provides some excellent scanning electron photomicrographs. Of the nine types, the fulcrate trophi of seisonids is not considered in this key. The other eight types, which are important to this key (cardate, forcipate, incudate, malleate, malleoramate, ramate, uncinate, and virgate), are briefly discussed below. They are also described in detail in Chapter 13 of Volume I.

Other important terms are defined below.

- **Alula**—Wing-shaped projections present at the base of each ramus.
- **Basal chamber**—Found in some trophi, a chamber or depression in the ramus with a window-like opening (basifenestra) that opens on the dorsal side.
- **Cardate trophi**—Trophi with a wide fulcrum and lyriform rami (U shaped).
- **Cirri**—Intermediate-length (cilia-like) structures that are present in the coronal region.
- **Forcipate trophi**—Trophi in the form of forceps that can be extruded from the mouth (found in some creeping and parasitic species; not planktonic and semiplanktonic); compare to Incudate.
- **Gelatinous tube**—A thick secretion from glands in the body that form a gelatinous mass that may remain transparent or become occluded with bacteria, algae, and/or detritus.
- **Hemiforcipate trophi**—The specialized jaws of Asciaporrectidae as described by De Smet (2006).
- **Hypopharyngeal muscle**—Powerful muscle in the mastax that helps in creating a strong pumping action in some species.
- **Incudate trophi**—The trophi of Asplanchnidae (planktonic and semiplanktonic) that possess large, cheliform rami, but reduced manubria and unci.
- **Illoricate**—A term used for rotifers with a thin body wall: one that is not thickened by the proteins of the intracytoplasmic lamina (compare to loricate).
- **Infundibulum**—A cup-shaped corona found in order Collothecacea.
- **Intramalleus**—An accessory part found in the trophi of some species; a connecting piece between the uncus and the manubrium.
- **Loricate**—A term used for rotifers with a thick body wall or lorica: one that is thickened by the proteins of the intracytoplasmic lamina; compare to illoricate.
- **Malleate trophi**—Trophi with a short fulcrum, but the manubrium and rami are strong; unci with four to seven teeth; compare to Malleoramate.
- **Malleoramate trophi**—Rami with strong teeth and unci with many slender teeth; compare to Malleate.
- **Modulus**—A specialized organ located at the anterioventral end of some Floscularia that makes small, round or bullet-shaped pellets (sometimes called pseudofecal pellets) that are composed of bacteria and tiny bits of detritus. The animal uses the pellets to construct a tall, turriform structure as found in many medieval castles. These pellets should not be confused with the fecal masses that a few species embed within a more extensive gelatinous tube.
- **Morphospecies**—A species designated and clearly separated from other species based on recognized unequivocal morphological features.
- **Oral plates**—An accessory part found in some trophi; plates with dentiform structures associated with the rami.
- **Oviferon**—A structure in Pentatrocha and Sinantherina that holds their parthenogenetic eggs.

- **Preunci**—An accessory part found in some trophi; a separate set of teeth present under the teeth in the uncus.
- **Pseudunci**—An accessory part of large hooked structures found in the trophi of family Birgeidae.
- **Ramate**—The trophi of bdelloid rotifers possessing wide, curved to crescentiform unci, but lacking the fulcrum.
- **Rostrum**—A small to prominent, beak-like structure that projects from the anterior end of rotifers, especially in some bdelloids.
- **Setae**—Very long cilia that line the edge of the corona (infundibulum) in Collotheca and the elongate arms (lobes) of Stephanoceros.
- **Spurs**—Short to long protrusions that project dorsally at the terminus of the foot. Note that the foot itself may be much shorter than the toes (compare toes).
- **Subbasal chamber**—A chamber or depression in the ramus with a fenestrate opening (subbasifenestra) on the ventral side.
- **Subunci**—An accessory part found in some trophi; a narrow rim of small fused bumps or ridges that are attached to the uncus near the teeth.
- **Sulcus**—A hollow depression where the lorica is not overly thickened, usually between two regions or plates where the lorica is thickened (see loricate).
- **Toes**—Short to long protrusions that project from the terminus of the foot in many rotifers (compare spurs).
- **Trochal pedicels**—Paired parts of the bdelloid corona elevated by a flexible stalk above the rest of the body.
- **Uncinate**—The trophi of collothecid rotifers, possessing well-developed rami, but weak fulcrum and manubria; three to five teeth in the unci.
- **Virgate**—Trophi with an action that functions in pumping; often asymmetrical with most elements having a tendency toward being slender; fulcrum and manubrium long.

MATERIAL PREPARATION AND PRESERVATION

Whenever possible, specimens should be examined alive and then studied after preservation to appreciate the consequence of fixation on body shape. This is especially important for bdelloids and illoricate monogononts, which will shrivel into a mass of tissue that is usually impossible to identify. While the trophi of these specimens may be extracted and used for identification, the details of the body are often needed as well. Solutions of sugar (40% sucrose) and 4% formalin (Haney & Hall, 1973) or ethanol (Black & Dodson, 2003), which are employed in the preservation of cladocerans, do not prevent contraction in rotifers. However, in loricate taxa, such as *Lecane*, formalin fixation is important. In this case a so-called hard fixation, with higher concentrations of formalin (>4%), will cause the tissues to contract, revealing the details of the surface of the lorica, which is critical to the identification to the level of species (Segers, 1995a). Visualization of preserved rotifers may be enhanced by the use of the stain Rose Bengal (Rublee & Partusch-Talley, 1995; Rublee, 1998). While molecular techniques are being used to identify cryptic species in rotifers, their use has not yet been applied to the routine identification of species.

As of yet there is no single anesthetic that has proved to be useful for a wide range of species. For example, carbonated water (club soda), 1% solution of $MgCl_2$, and various other narcotizing agents have been tried with mixed success. For a review of these techniques consult the following publications: Edmondson (1959), Nogrady & Rowe (1993), Wallace et al. (2006), as well as Chapter 13 in Volume I. Two older techniques that kill the specimen in more or less natural condition are the hot water fixation technique of Edmondson (1959) and the formalin drop technique. However, both require much practice to master. In the latter procedure, minute drops of formalin (<5 μL) are added over a long period of time (hours) to a small volume of water (~1 mL) in which a specimen is kept. For additional information on preservation, storage, and mounting consult Wallace et al. (2006) and Jersabek et al. (2010).

Identification of rotifers usually requires examination of the live animal, which is then followed by close study of their trophi. However, for some taxa, such as the Asplanchnidae, identification to genus (*Asplanchna, Asplanchnopus,* and *Harringia*) is quite simple and requires only rudimentary understanding of rotifer morphology. On the other hand, while one can easily become familiar with the body form of subclass Bdelloidea or the monogeneric Lecanidae (*Lecane*), identification to species is challenging. In many cases it will be necessary to extract the trophi using bleach (sodium hypochlorite), which dissolves the animal's soft tissues. Edmondson's (1959) description of the extraction employs a depression slide to begin the process, but that necessitates moving the trophi from the depression slide to a flat slide after the soft tissues have disappeared. With practice this method works well, and it has the added advantage of being able to wash the bleach away while the trophi are in the well of the slide. Alternatively, the animal can be placed on a flat slide in a drop of water. To this a small drop of bleach is added and a cover glass is careful applied to the preparation. The animal is observed as the bleach dissolves its tissues, but observers must be diligent as this can happen quite suddenly. Confounding this process is the fact that bubbles usually form, obscuring the view. This technique also works without adding the cover glass. In that case, the trophi must be located and then some of the bleach solution is removed with a micropipette followed by the slow addition of clean

water. That process is then repeated several times to wash away the bleach, which otherwise will continue its hydrolysis of the trophi. At this point a cover glass may be gently added and the trophi examined. This slide will last until the liquid evaporates from under the cover glass. For a longer-lasting preparation the fluid must be replaced with a glycerol +4% formalin solution. To do this, prepare a series of 4% formalin solutions in increasing concentrations of glycerol: 10, 20, 30 … 100%. Employing the same technique used to remove the bleach water, the liquid is slowly replaced (over an hour or more) with the graded 4% formalin−glycerol series. Such preparations will last for days, if not longer. However, this preparation can be made to last longer by sealing the cover glass to the slide by applying a line of melted Vaspar (a 50:50 mixture of melted paraffin wax and petroleum jelly) to the four edges of the cover glass. Finally, it must be remembered that the trophi are tiny (<50 μm), delicate structures composed of six to seven elements (see above) that have a precise three-dimensional arrangement.

Interpreting whether the body wall is thickened (loricate) or not (illoricate) can be difficult and it does take some experience to judge this characteristic in forms that do not easily fall one way or the other. To get an indication as to how firm the lorica is, follow this procedure. When working with fresh material apply gentle pressure from the point of a pencil or probe onto the cover glass while observing the specimen. If the body puffs out under pressure and returns to its original shape when the pressure is released, the specimen is illoricate. Loricate forms will exhibit much less flexibility of the body wall. That is, when pressure is applied to the cover glass the animal does not puff out. However, if too much pressure is applied to the cover glass, the animal may be crushed, becoming irreversibly damaged, perhaps rendering them unidentifiable. In preserved materials, illoricate forms tend to shrivel up, while the body wall of loricate rotifers will retain its shape even if the inner organs separate from the body wall, collapsing into a central mass of tissue. Some members of the Brachionidae that are weakly loricate may key to the Epiphanidae.

KEY TO ROTIFERS

Rotifera: Subclasses

1	Rotifers with ramate trophi (Fig. 13.11t in Volume I) and paired ovaries; usually not planktonic in open waters; movement along surfaces often in a leech-like fashion	**Bdelloidea**
	[Although this step obviously is very important, special care is generally not necessary to resolve this point. The ramate trophi of bdelloids, which lack the fulcrum and have the largest unci teeth in the middle, are usually identifiable in whole animals without resorting to isolating the trophi from the animal (Ricci and Melone 2000, Fontaneto et al. 2007c). If the type of trophi and number of ovaries cannot be determined, there are other clues that may be useful for live organisms. Upon contacting a substratum, many bdelloids will crawl on the surface in a manner reminiscent of a leech, hence the etymon of the name (Greek, *bdella*, leech). Furthermore, some bdelloids possess a corona that has the appearance of two separate wheels elevated on short stalks (pedicles), while only a few monogononts of the Flosculariidae give this impression, and most of those are permanently sessile.]	
1′	Rotifers with a single ovary; trophi other than ramate:	**Monogononta**

Rotifera: Bdelloidea: Families

Important keys to the bdelloids include the following: Bartoš (1951), Edmondson (1959), Donner (1965), Koste & Shiel (1986), Ricci & Melone (2000), Kutikova (2005), and Wallace et al. (2006). Estimates of the number of species reported here are probably too low. This is no doubt due to the fact that there are few taxonomists currently working with bdelloids in the Palearctic. Four genera not reported from this region are included here for completeness and to call attention to the need for additional research. The monospecific marine genus, *Zelinkiella* (Philodinidae), is not included.

1	Stomach with lumen	2
1′	Stomach without lumen, as a syncytial mass of food vacuoles that gives the gut a frothy appearance	**Habrotrochidae**
	[The food vacuoles must not to be confused with oil droplets that are often present in other bdelloids or with the symbiotic algae in the stomach wall of Ituridae (*Itura*; Subclass Monogononta: Order Ploima).]	
2(1)	Trophi located deeper, not near the mouth and are not exsertile	3
2′	Trophi located near the mouth and are exsertile (protruded during feeding)	**Philodinavidae**
3(2)	Corona with paired trochal disks on raised pedicles.	**Philodinidae**
3′	Corona lacking trochal disks (no pedicles); ventrally a pair of flat, ciliated fields separated by a longitudinal groove.	**Adinetidae**

Rotifera: Bdelloidea: Habrotrochidae: Genera

1	Ring on trochal pedicels absent 2
1′	Shelf-like ring present on the trochal pedicels (Fig. 8.2), but may not extend corona to feed; 6–10 teeth on each uncus; 200–500 µm; habitat mostly in soil water ..... *Otostephanos*
2(1)	Each trochus partially covered by a wide, dorsal, membrane-like hood seen when the animal is feeding (Fig. 8.3); 3–9 teeth on each uncus; ~200 µm; habitat mostly soil and on mosses ..... *Scepanotrocha*
2′	Hood extending over trochus is absent (Fig. 8.4); ≥10 teeth on each uncus of varying width; 150–400 µm; habitat aquatic sediments, soils, and mosses ..... *Habrotrocha*

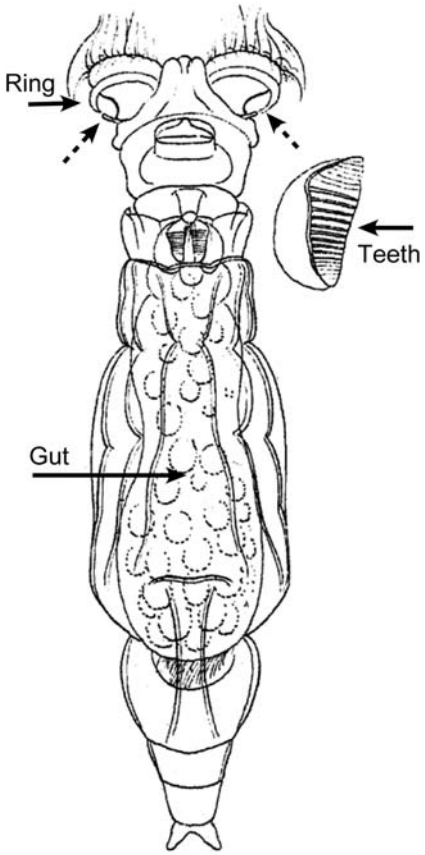


FIGURE 8.2 Habrotrochidae: *Otostephanos*. *Dashed arrows* = pedicles (PAL). *After Murray 1911.*



FIGURE 8.3 Habrotrochidae: *Scepanotrocha rubra*. Bar = 50 µm (PAL). *After Bryce 1910.*

Rotifera: Bdelloidea: Philodinavidae: Genera

1	Corona reduced, with only a hint of being bilobed or not bilobed 2
1′	Corona a poorly developed bilobed-disk on short pedicels, lacking upper and lower lips (Fig. 8.5); ~500 µm; ephemeral habitats ..... *Abrochtha intermedia* (Beauchamp, 1909)
2(1)	Corona possessing two small, ciliated disks on the ventral side (Fig. 8.6); ~130–300 µm, habitat includes mosses and algae ..... *Henoceros*
2′	Corona with even greater reduction (no wheel-like structure present); cilia are restricted to a small region around the mouth (Fig. 8.7); ~200–300 µm; habitat includes mosses in well-oxygenated streams ..... *Philodinavus paradoxus* (Murray, 1905)

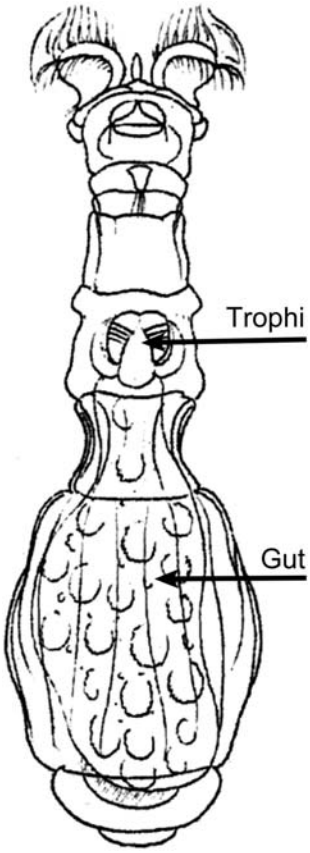


FIGURE 8.4 Habrotrochidae: *Habrotrocha* (PAL). *After Murray 1911.*

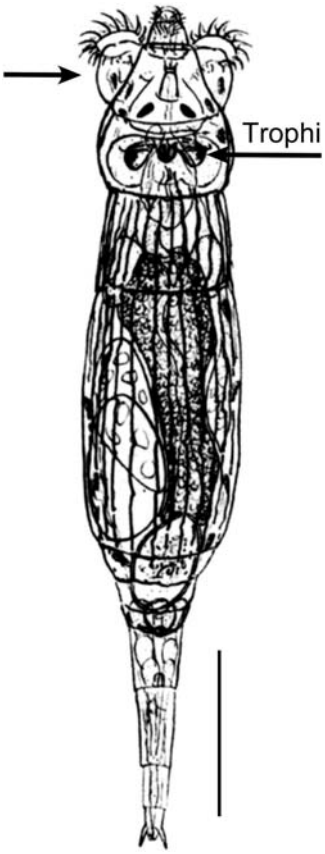


FIGURE 8.5 Philodinavidae: *Abrochtha intermedia.* Arrows: corona: bilobed-disk on short pedicels and trophi. Bar = 100 µm (PAL). *After de Beauchamp 1909.*



FIGURE 8.6 Philodinavidae: *Henoceros*. Left side view. Bar = 50 µm (PAL). *After Milne 1916.*

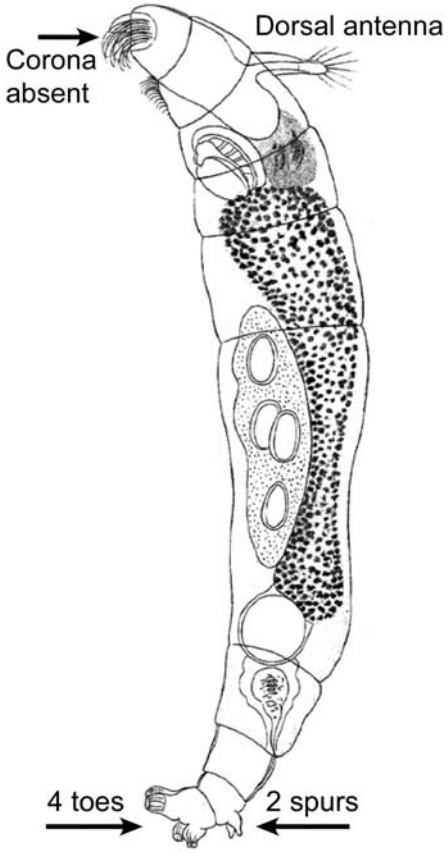


FIGURE 8.7 Philodinavidae: *Philodinavus paradoxus.* Animal 200−300 µm (PAL). *After Murray 1905.*

Rotifera: Bdelloidea: Philodinidae: Genera

1	Toes absent, but with an attachment disk on the terminal foot joint	2
1′	Toes present on foot: numbering 2, 3, or 4 [One must take great care to distinguish toes (extensions of the pedal glands) from spurs (stiff, conical appendages lacking pedal bland ducts) (Ricci & Melone, 2000).]	3
2(1)	Spurs on caudal region of foot exceptionally small (only mere bumps); one major tooth on each unci; >500 µm; obligatorily epizoic on freshwater crabs (*Potamon*)	*Anomopus*
2′	Spurs on caudal region of foot not exceptionally small; corona wide; toes absent (Fig. 8.8); usually ≥3 up to 10 teeth; 200–600 µm; on mosses, some epizoic; lives in the water film of soils and mosses	*Mniobia*
3(1)	More than two toes on foot	4
3′	Two toes on foot; eyespots absent; c. 400 µm; (Fig. 8.9)	*Didymodactylos carnosus* Milne, 1916
4 (3)	Three toes on foot	5
4′	Four toes on foot	7
5(4)	Edges of corona without horns or wing-shaped projections	6

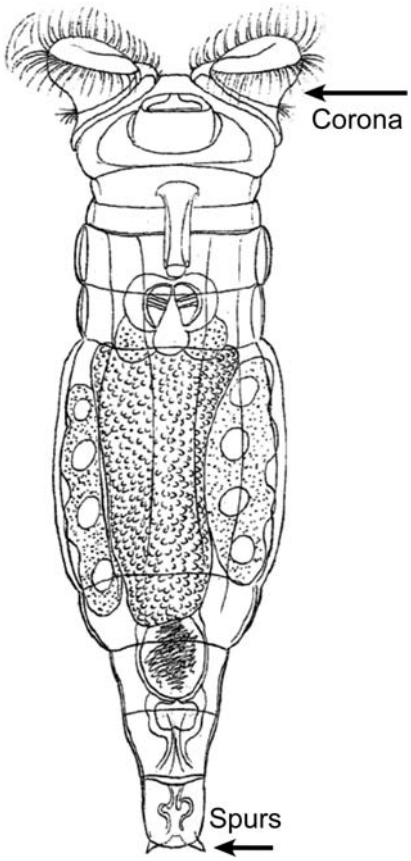


FIGURE 8.8 Philodinidae: *Mniobia* (PAL). *After Murray 1905.*

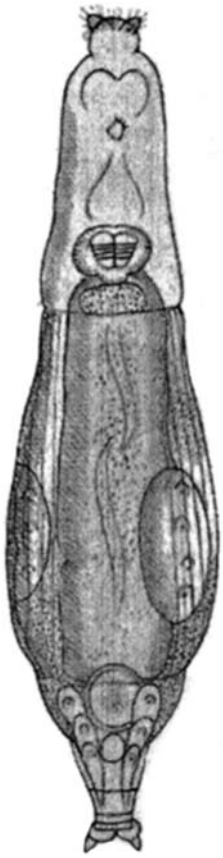


FIGURE 8.9 Philodinidae: *Didymodactylos carnosus* (PAL). *After Milne 1916.*

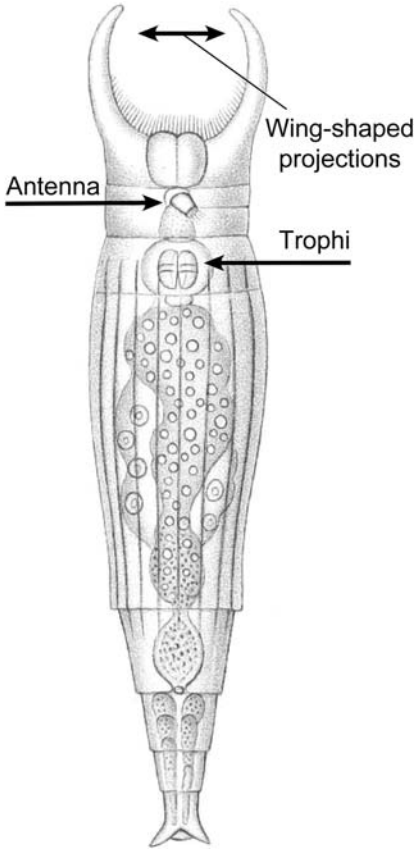


FIGURE 8.10 Philodinidae: *Ceratotrocha.* Animals 150−350 µm (PAL). *After Weber 1898.*

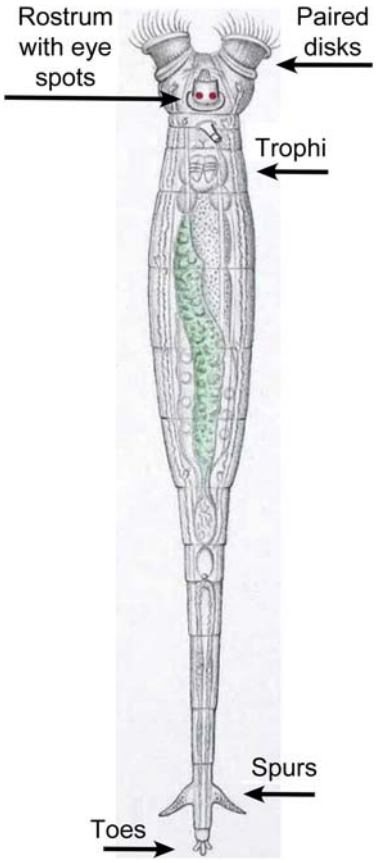


FIGURE 8.11 Philodinidae: *Rotaria* (PAL). *After Weber 1898.*

5′	Edges of corona expanded into prominent, elongate, conical, or alate projections; 2−3 teeth on each uncus (Fig. 8.10); 150−350 µm; habitat is the interstitial water films of soils ..... *Ceratotrocha*
6(5)	Rostrum (eyes often present), spurs, toes, and dorsal antenna prominent; three toes and two long spurs (Fig. 8.11); uncus with two, rarely three teeth; ≤400−1600 µm; ovoviviparous; free swimming; habitat mostly water bodies ..... *Rotaria*
6′	Rostrum, spurs, toes (three short), and dorsal antenna not prominent (Fig. 8.12); surface may be sculptured; unci with two, three, rarely five teeth; 200−500 µm; oviparous; habitats include aquatic sediments and the interstitial film of soils and mosses ..... *Macrotrachela*
7(4)	Integument of trunk stiff (somewhat inflexible) and sculptured 8
7	Integument of trunk thin and flexible 9
8(7)	Spurs long; many species possess eyespots (Fig. 8.13); stiff spines usually present on body; foot long, often with long spurs; 300−500 µm; ovoviviparous; usually living in aquatic sediments ..... *Dissotrocha*
8′	Spurs short; eyespots absent (Fig. 8.14); body stiff and armor-like; foot short with four toes; 200−400 µm; oviparous; interstitial film on mosses ..... *Pleuretra*
9(7)	Spurs very long, flat and wide; foot ≥1/2 of total animal length (Fig. 8.15); 250−650 µm; oviparous or ovoviviparous; often epizoic on crustaceans ..... *Embata*
9′	Spurs short or, if long, not flat and wide; foot ≤1/2 of total animal's length (Fig. 8.16); unci usually with two or more teeth; 100−800 µm; ponds and lakes and in the interstitial water film of soils and mosses ..... *Philodina*

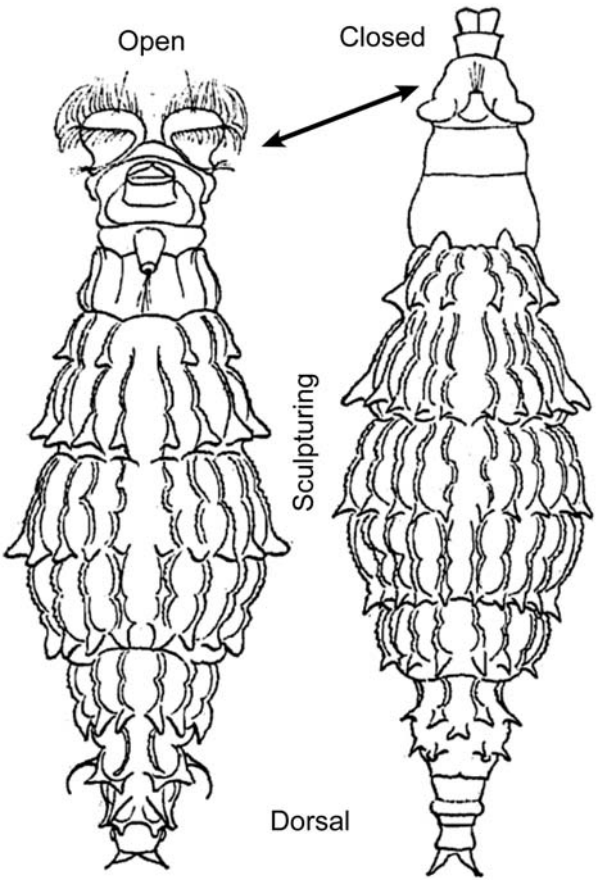


FIGURE 8.12 Philodinidae: *Macrotrachela* (PAL). *After Murray 1911.*

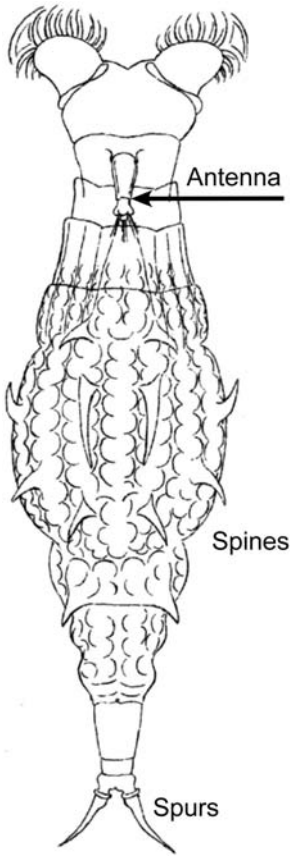


FIGURE 8.13 Philodinidae: *Dissotrocha* (PAL). *After Murray 1908.*



FIGURE 8.14 Philodinidae: *Pleuretra*. Adult bars ~100 µm. Insert: trophi, bar ~20 µm.

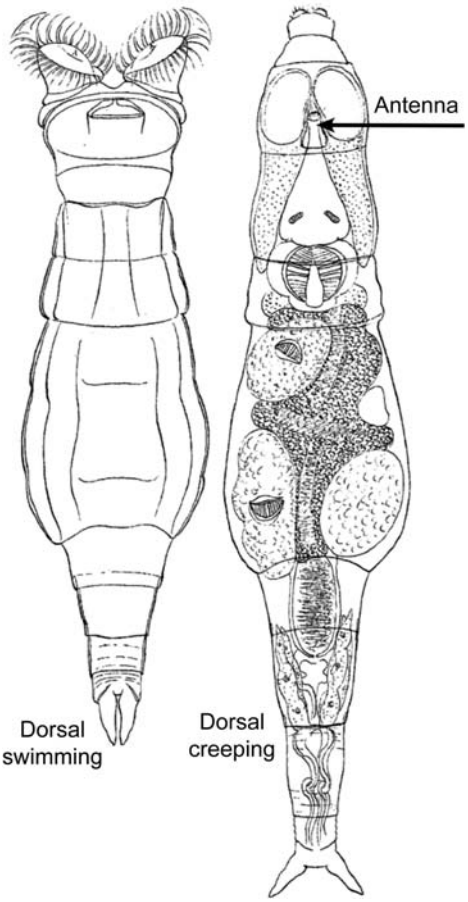


FIGURE 8.15 Philodinidae: *Embata* (PAL). *After Murray 1905.*

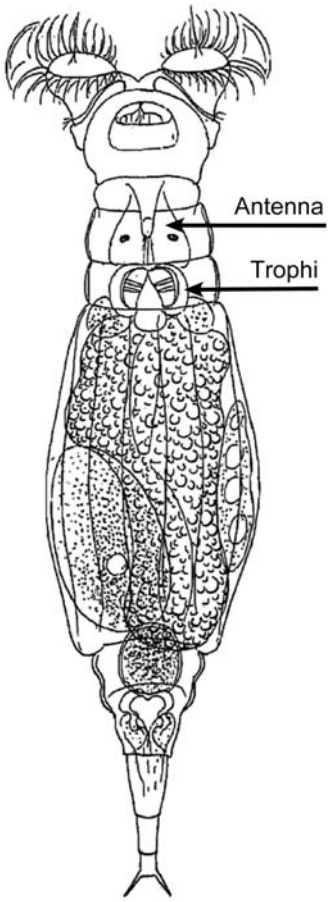


FIGURE 8.16 Philodinidae: *Philodina* (PAL). *After Murray 1906.*

Rotifera: Bdelloidea: Adinetidae: Genera

1	Body fusiform, with distinct foot possessing two spurs (Fig. 8.17); corona developed as a ventral ciliate field, possesses a rake that it uses to collect food; trophi small, unci with two teeth; body dorsoventrally compressed; foot well develop; does not swim; 200–700 µm; habitat includes aquatic sediments and the interstitial film of mosses, lichens, and soils ..... *Adineta*
1′	Body vermiform possessing an indistinct foot lacking spurs, but with foot terminus bearing 10–12 papillae (Fig. 8.18) 175–250 µm ..... *Bradyscela*

Rotifera: Monogonata: Orders

1	Trophi other than uncinate; corona with typical ciliated lobes or fields, or ciliated bands 2
1′	Trophi uncinate (Fig. 13.10h in Volume I); corona lacking typical ciliated regions, but is open as a small to large cup-shaped structure (infundibulum) with or without elongate setae (sometimes with cilia as well) around the margin (Fig. 13.8 in Volume I) ..... **Collothecacea**
2(1)	Rotifers possessing malleoramate trophi (Fig. 13.11i in Volume I) ..... **Flosculariaceae** [Malleoramate trophi possess a fulcrum, crescentiform manubria, and unci with a few clavate to numerous fine teeth nearly completely overlying the rami (compare to description in the key to Ploima); teeth close to the fulcrum are usually larger than those more distant. In live animals, the nearly constant movement of the trophi in a grinding or pounding-like action is characteristic.]
2′	Rotifers with trophi other than malleoramate ..... **Ploima**

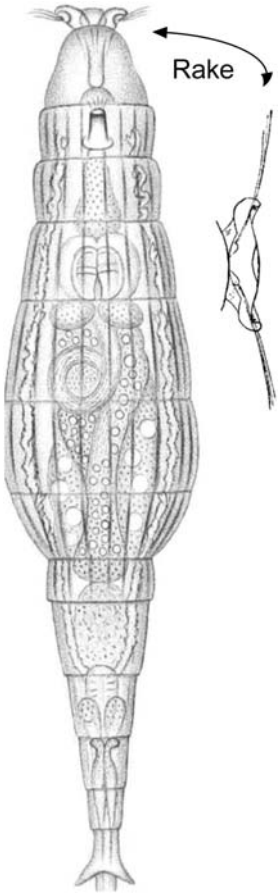


FIGURE 8.17 Philodinidae: *Adineta* (PAL). *After Janson 1893.*



FIGURE 8.18 Philodinidae: *Bradyscela* (PAL). *After Bryce, 1893.*

Rotifera: Monogonata: Collothecacea: Families

Important keys to the Collothecacea include the following: Bērziņš (1951) and Meksuwan et al. (2013).

1 Coronal margin of adults usually with long setae (sometimes absent) and/or ciliated; living in transparent gelatinous tubes; mostly sessile, but some planktonic in open waters ..... **Collothecidae**

1′ Coronal margin of adults without setae or cilia; with or without gelatinous tube ..... **Atrochidae**

Rotifera: Monogonata: Collothecacea: Collothecidae: Genera

1 Corona with very elongate lobes resembling arms, approximately as long as trunk; arms either stout with robust setae arranged in whorls and held at right angles to arms or slender with long slender setae not arranged in whorls; ≤1500 µm; sessile (Fig. 8.19) ..... *Stephanoceros*

[In light of the fact that some members of the genus *Collotheca* also possess elongate lobes, Meksuwan et al. (2013) have recommended that the status of both genera be re-evaluated.]

1′ Corona lobes long, short, or absent; setae never in whorls; clear tube may be embedded with algae or covered with debris (Fig. 8.20); ~100−2500 µm ..... *Collotheca*

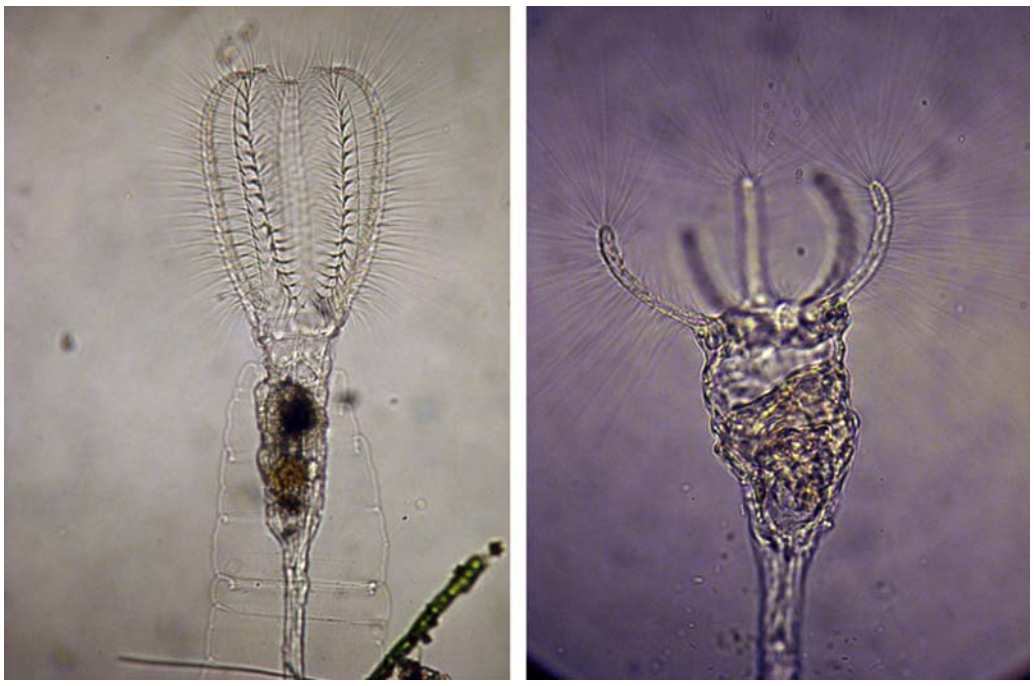


FIGURE 8.19 Collothecidae: *Stephanoceros fimbriatus* (left) and *Stephanoceros millsii* (right). Animals c. 1000 µm. *Photomicrographs courtesy of Adele Hochberg, University Massachusetts at Lowell USA.*

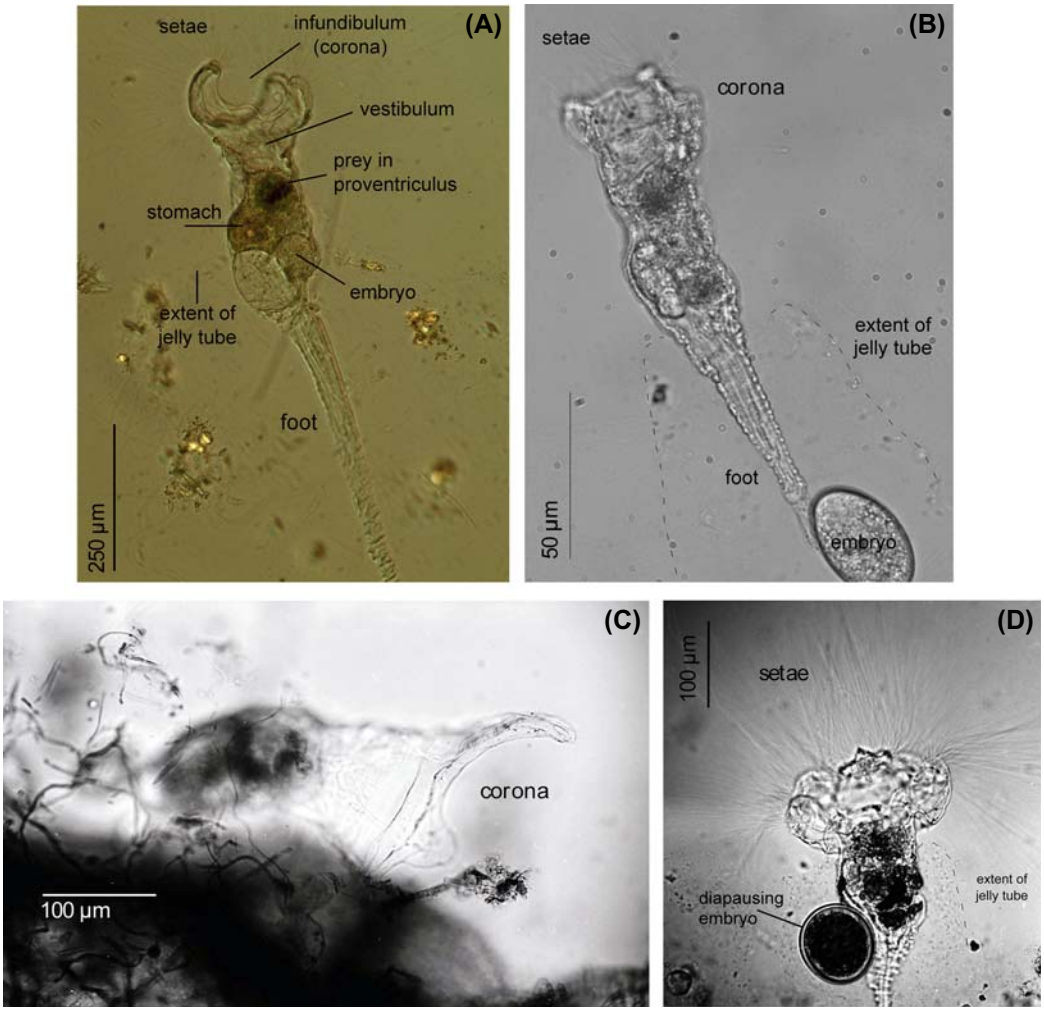


FIGURE 8.20 Collothecidae: (A) *Collotheca trilobata*, a sessile species; (B) *Collotheca libera* with one embryo, a planktonic species; (C) *Collotheca ferox*, a sessile species; (D) *Collotheca* sp., with one diapausing embryo. Scale bars as illustrated.

Rotifera: Monogonata: Collothecacea: Atrochidae: Genera

1 Coronal not large and bowl-shaped; sessile or mobile; trunk elongated; foot not a short stalk 2

1′ Corona large and bowl-shaped, as wide as trunk of animal; trunk (body) as a slightly flattened sphere; mouth (infundibulum) positioned parallel to substratum (≤1 mm); sessile, attached to substratum by a short, flexible centrally positioned, ventral foot (Fig. 8.21) .... *Cupelopagis vorax* (Leidy, 1857)

2(1) Corona with a long dorsal lobe; transparent gelatinous tube; foot relatively short; ≤1500 µm; sessile, often present in colonies of *Sinantherina socialis* (Flosculariidae) on whose young it feeds (Fig. 8.22) ..... *Acyclus inquietus* Leidy, 1882

2′ Corona lacking the long dorsal lobe, but possessing horny process on dorsal side; tube lacking; foot short and hemispherical in shape; 1200−1500 µm; mobile (Fig. 8.23) ..... *Atrochus tentaculatus* Wierzejski, 1893

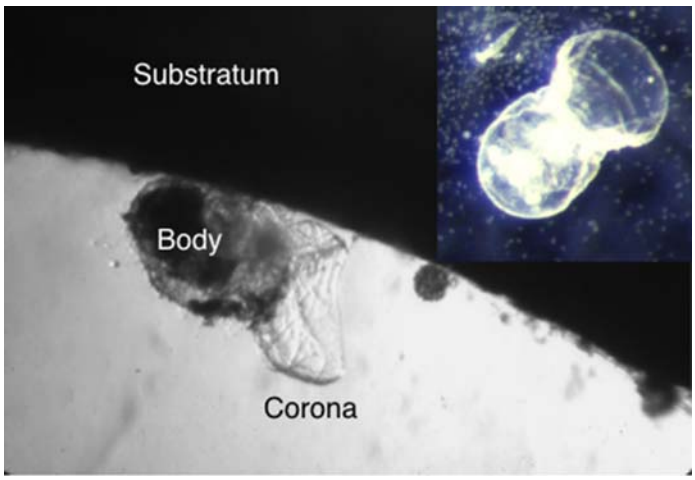


FIGURE 8.21 Atrochidae: *Cupelopagis vorax*. Side view: animal attached to the undersurface of a hydrophyte; insert: from above, animal attached in a Petri dish. Body, without corona ~250 µm.

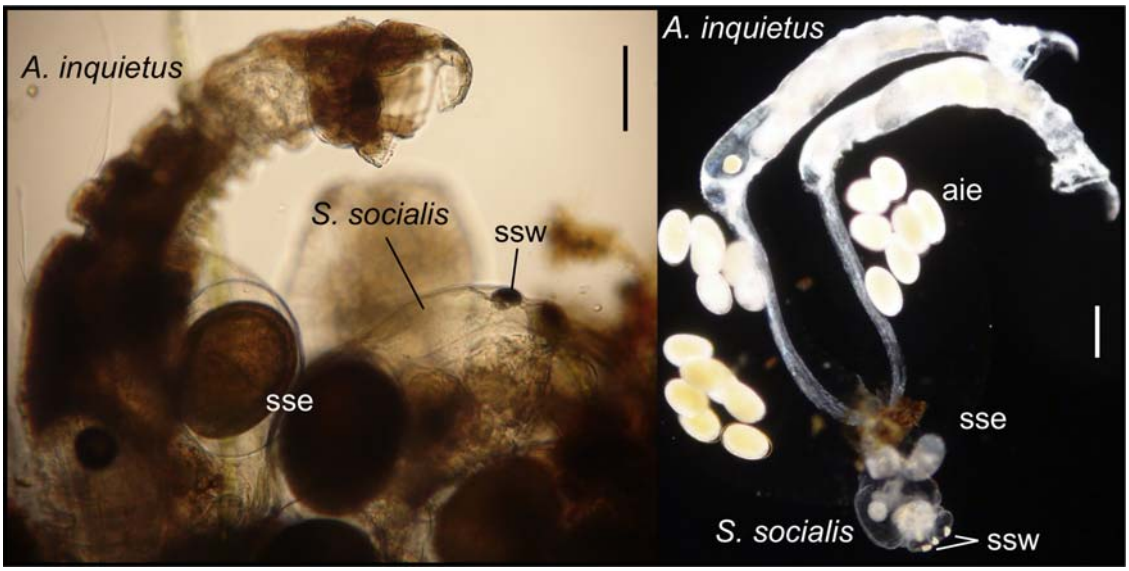


FIGURE 8.22 Atrochidae: *Acyclus inquietus.* Animal within a colony of *S. socialis* (left); two adult *Acyclus* attached to a bit of substrate along with one *S. socialis* (right). Abbreviations: sse = *S. socialis* embryos; ssw = *S. socialis* warts; aie = *A. inquietus* embryos. Bars ~100 µm. *Photomicrographs courtesy of Adele Hochberg, University Massachusetts at Lowell.*

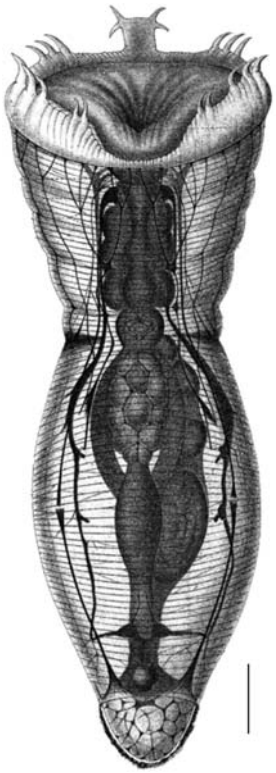


FIGURE 8.23 Atrochidae: *Atrochus tentaculus*. Ventral view. Bar = 100 µm (PAL). *After Wierzejski 1893.*

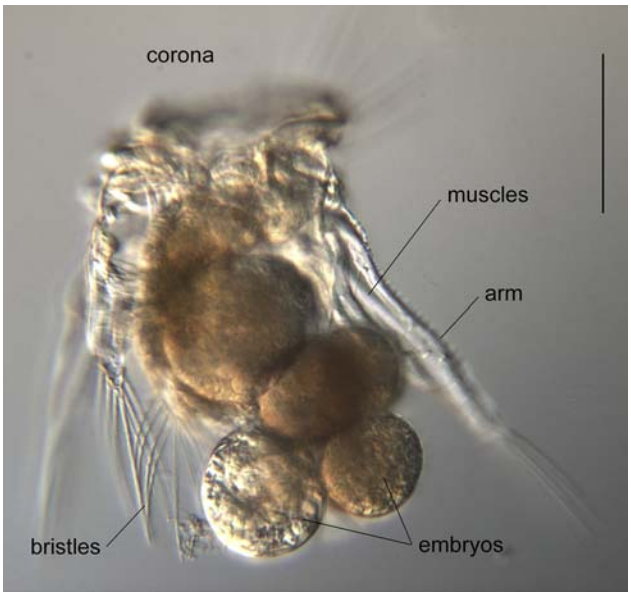


FIGURE 8.24 Hexarthridae: *Hexarthra*. Bar = 100 µm.

Rotifera: Monogononta: Flosculariaceae: Families

Important keys and other taxonomic papers on the Flosculariaceae include the following: Edmondson (1949), Segers (1997), Segers & Wallace (2001), Segers & Shiel (2008), and Segers et al. (2010). The monospecific genus *Pentatrocha* is not included herein as it has not been reported from the Palaearctic (Segers & Shiel, 2008; Meksuwan et al., 2011).

1	Body lacking hollow, arm-like, setose appendages; planktonic or sessile 2
1′	Conical body with six arm-like, setose appendages that are outgrowths of the body wall; appendages inserted with powerful swimming muscles (Fig. 8.24); ~100–400 µm; exclusively planktonic ..... Hexarthridae, *Hexarthra*
2(1)	Planktonic or not; solitary or colonial; lacking signature trophi described below and conical body of the Conochilidae 3
2′	Planktonic, conical, illoricate animals within a loose gelatinous matrix; gut is lyriform with anus exiting above the jelly margin when the animal is extended; foot unsegmented; trophi unique, possessing asymmetrical unci, right unci teeth with intercalating projections; proximal projection of right manubrium well developed, connecting to both ramus and proximal tooth of uncus plate .... **Conochilidae**
3(2)	Rotifers lacking a large, circular to lobate, auriciform corona 4
3′	Rotifers typically with elongate bodies and large, circular (slightly elliptical) to lobate, cordiform, or auriciform corona; solitary or colonial; with or without a tube or gelatinous matrix; mostly sessile, but some free-swimming ..... **Flosculariidae**
4(3)	Without movable anterior spines (bristles) below the corona; body spherical, with a corona as a circular band of cilia around the equator, or body oviform, with corona a slight extension of the body; **OR** with two movable anterior spines (bristles) below the corona, of varying lengths often much longer than the body and one (rarely two) rigid caudal spines; foot absent ..... **Trochosphaeridae**
4′	Rotifers never spherical in shape; without long spines (bristles) below the corona ..... **Testudinellidae**

Rotifera: Monogononta: Flosculariaceae: Conochilidae: Genera

This family (Segers & Wallace, 2001) comprises <12 species forming autorecruitive colonies (Chapter 13, Volume I) of an adult and 1–3 recently hatched young or colonies of from 5 to 100 individuals; occasionally enormous colonies (>400 individuals) of *C. unicornis* occur. Subitaneous eggs are deposited in jelly where they remain for a short period before hatching. Meksuwan et al. (2015) discuss the phylogenetic position of the family.

1 Corona lyriform possessing a ventral gap in the ciliation 2

1′ Coronal other; colonies of 30–60 adults and juveniles; colonies ~1 mm in diameter (in the Nearctic, this species has only been reported from rice paddies in USA (LA) ..... *Conochilopsis causeyae* (Vidrine, McLaughlin & Willis, 1985)

2(1) Corona slanted ventrally to body axis; antennae located inside corona field; diapausing egg smooth; colonies of more or less spherical (Fig. 8.25) ..... *Conochilus* (Subgenus *Conochilus*)

2′ Corona perpendicular to body axis; antennae located dorsally outside of the coronal field; diapausing eggs are ornamented with spirals; colonies not spherical, typically an adult with none to three juveniles; colony's gelatinous matrix usually colonized by euglenoid algae (Fig. 8.26) ..... *Conochilus* (Subgenus *Conochiloides*)

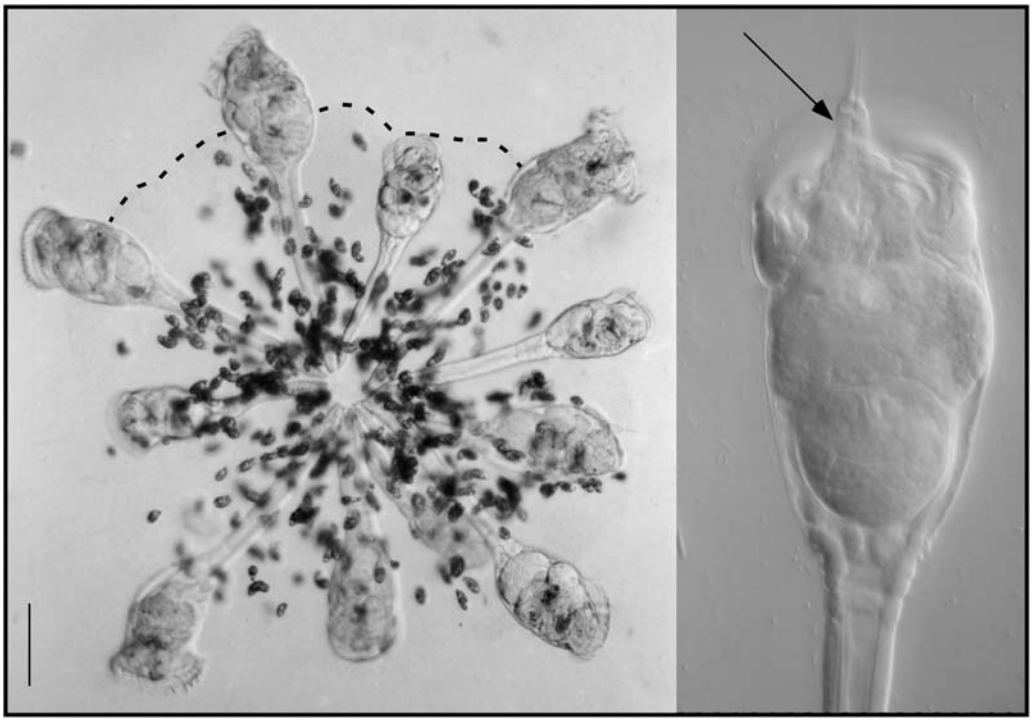


FIGURE 8.25 Conochilidae: Small colony of *Conochilus* (*Conochilus*) *unicornis* (left). Dashed lines partially outline the margin of the gelatinous matrix. Dark ovoid objects are euglenoid algae colonizing the gelatinous matrix. Individual *C. unicornis* (right). *Arrow* = fused antennae within the corona. Bar = 100 μm.

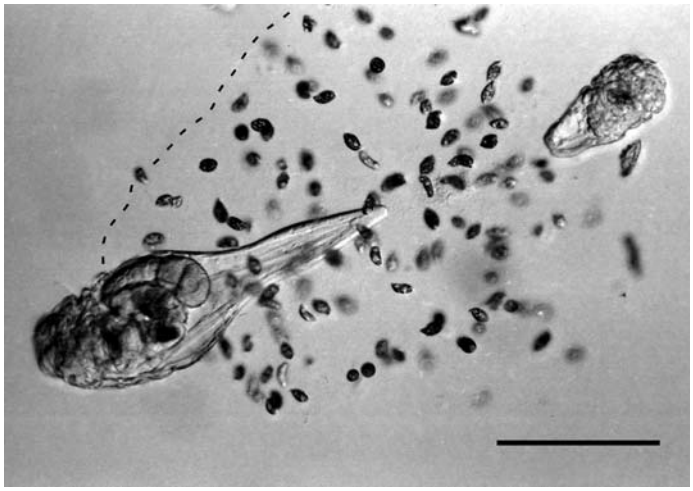


FIGURE 8.26 Conochilidae: *Conochilus* (*Conochiloides*): an adult with one juvenile. Dashed lines partially outline the margin of the gelatinous matrix. Dark ovoid objects are euglenoid algae colonizing the gelatinous matrix. Bar = 250 μm.

Rotifera: Monogononta: Flosculariaceae: Flosculariidae: Genera

1	Dorsal antennae (paired), not conspicuously long, but not visible when animal contracts 2
1′	Single, centrally placed, dorsal antenna, conspicuously long (longer than body width), visible when animal is contracted, ≤500 µm (Fig. 8.27) ..... *Beauchampia crucigera* (Dutrochet, 1812)
2(1)	Corona with one or more pairs of distinct auriciform lateral lobes 3
2′	Corona without distinct auriciform lobes (corona circular, subcircular, or at most lobes indistinct to cordiform) 6
3	Corona with more than one pair of distinct lateral lobes on each side of the animal; tube a gelatinous matrix with or without pellets or debris 4
3′	Corona with one pair of distinct lateral lobes on each side of the animal; animals usually solitary (occasionally small colonies, usually ≤12) in separate straight or slightly curved tubes, each formed as a distinct pipe of hardened secretions (Fig. 8.28); two species with ringed tubes; three species with tubes as a granular matrix (stucco like); ≤1000 µm ..... *Limnias*
4(3)	Corona very large with more than four lobes 5
4′	Corona large with two pairs of distinct lateral lobes (=four lobes), one pair above the other; animals often colonial (Fig. 8.29); ≤1500 µm ..... *Floscularia*
5	Corona with four pairs of distinct lateral lobes (=eight lobes), one pair smaller, solitary in a gelatinous tube (Fig. 8.30); 200–2000 µm ..... *Octotrocha speciosa* Thorpe, 1893 [Potential confusion over identification of this species warrants additional taxonomic study. For comments and additional illustrations consult Segers & Shiel (2008), Segers et al. (2010), and Meksuwan et al. (2011).]
5′	Corona with five promanent and two small lobes; solitary or colonial in a gelatinous tube; ≤1300 µm; consult Meksuwan et al. (2011) for figures and additional details ..... *Lacinularoides coloniensis* (Colledge, 1918) [This species is included in the key as it may be confused with *Octotrocha speciosa.*]
6(2)	Corona cordiform (reniform), subquadrangular, or occasionally round; animals usually forming spherical to ellipsoid colonies with many individuals, occasionally solitary; tube, when present, a continuous gelatinous matrix 7
6′	Corona round to slightly elliptical, or weakly lobed; animals usually solitary in separate, gelatinous tubes that may be covered by or infiltrated with debris (Fig. 8.31); 150–1000 µm ..... *Ptygura*
7(6)	Possessing a specialized egg-bearing structure (oviferon, ovifer) below anus to which eggs attach; solitary or colonial; sessile or planktonic; gelatinous matrix is absent (minimal?); individuals: 400–2000 µm, colonies: ≤4 mm (Fig. 8.32) ..... *Sinantherina*
7′	Lacking an oviferon; usually colonial; sessile or planktonic; possessing gelatinous matrix; individuals: ≤2000 µm, colonies: ≤ 5 mm (Fig. 8.33) ..... *Lacinularia*

Rotifera: Monogononta: Flosculariaceae: Trochosphaeridae: Genera

Consult Nogrady & Segers (2002) for details of this family.

1	Body spherical or oviform 2
1′	Rotifers not as above; possessing two movable anterior setae (bristles or spines) of varying lengths below the corona, often much longer than the body and one (rarely two) rigid caudal spines; foot absent (Fig. 8.34); excluding setae ~40–325 µm ..... *Filinia*
2(1)	Body spherical, corona as a circular band of cilia around the equator or offset toward one end; 320–1100 µm; viviparous; (Fig. 8.35 A) ..... *Trochosphaera*
2′	Body oviform; corona a slight extension of the body; ~125 × 160 µm; oviparous (Fig. 8.35 B) ..... *Horaella brehmi* Donner, 1949

Rotifera: Monogononta: Flosculariaceae: Testudinellidae: Genera

1	Lorica greatly flattened dorsoventrally with dorsal and ventral plates fused along the lateral margin (Fig. 8.36 A); foot annulated and retractile; ≤250 µm ..... *Testudinella*
1′	Lorica not greatly flattened, rather possess four nearly equal lobes in cross-section; one pair frontal eyespots; foot absent (Fig. 8.36 B); ≤120 µm ..... *Pompholyx*



FIGURE 8.27 Flosculariidae: *Beauchampia.* Bar = 100 µm.

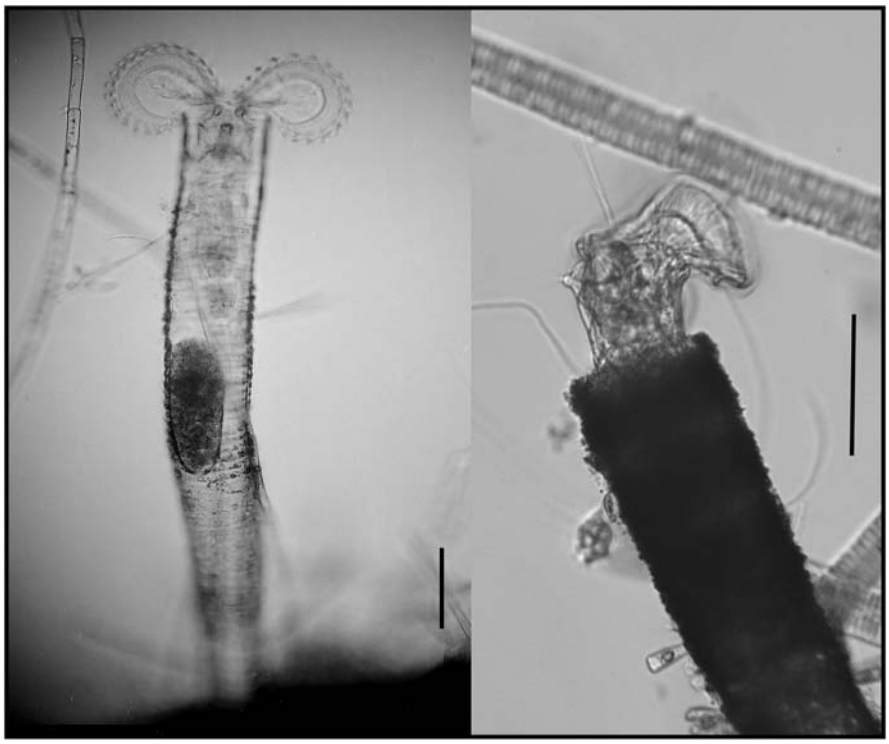


FIGURE 8.28 Flosculariidae: *Limnias melicerta* (left) and *Limnias ceratophylli* (right). Bars = 100 µm.



FIGURE 8.29 Floscullariidae: *Floscularia conifera,* small colony (left); *Floscularia ringens,* anterior (center); *Floscularia janus* (right). Bars = 100 µm. *Center photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso.*



FIGURE 8.30 Floscullariidae: *Octotrocha speciosa.* Solitary individual in a gelatinous tube. Bar = 250 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso.*

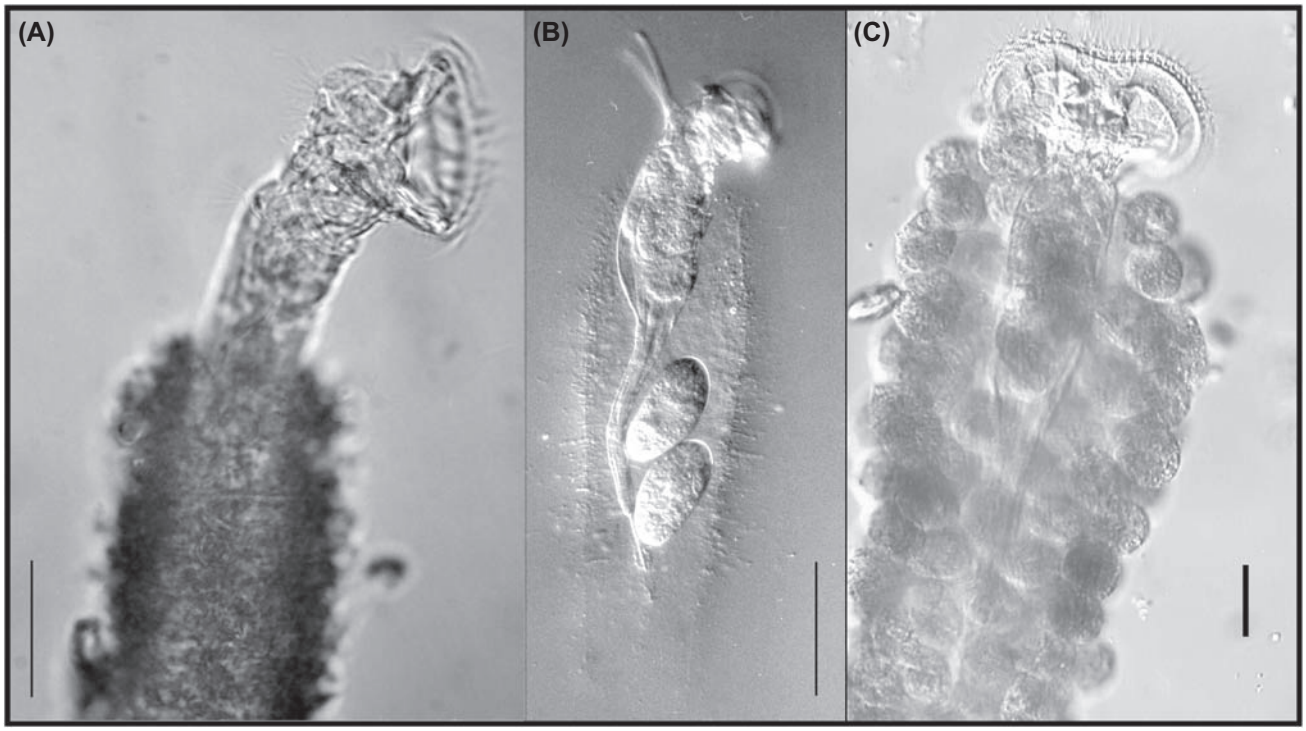


FIGURE 8.31 Flosculariidae: *Ptygura beauchampi* (sessile), *Ptygura libera* (planktonic, with two embryos), and *Ptygura pilula* (sessile, with fecal pellets embedded in a gelatinous tube). Bars = 50 µm.

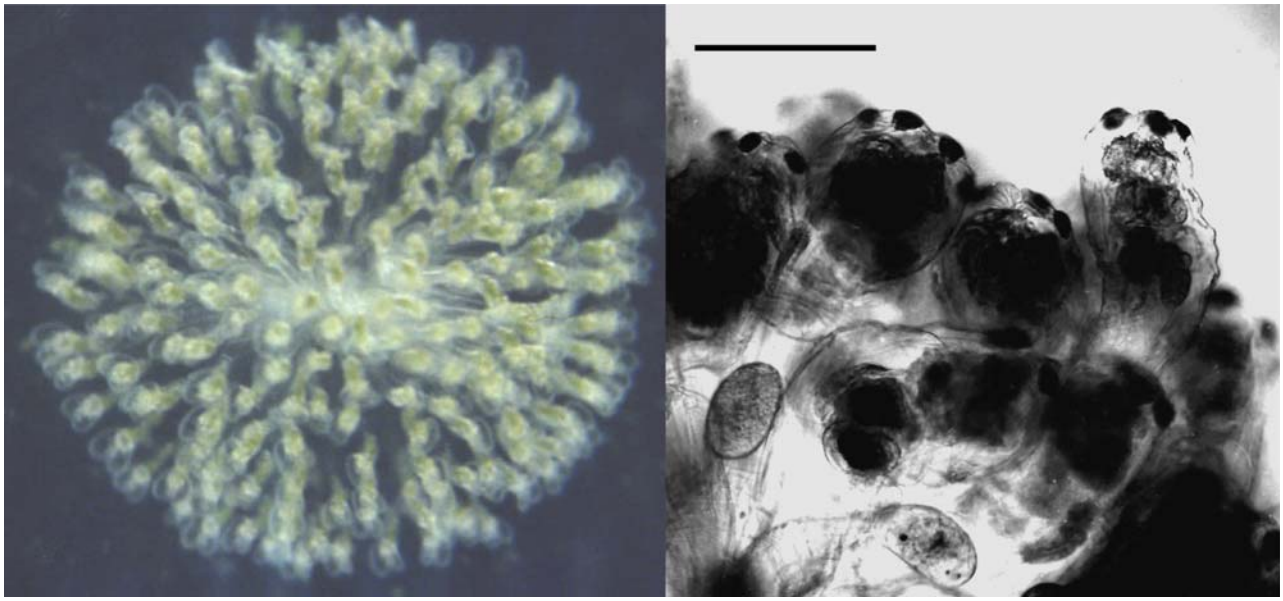


FIGURE 8.32 Flosculariidae: *Sinantherina socialis,* entire colony (left) ≥1 mm diameter and close up of a portion (right). Bar = 200 µm.

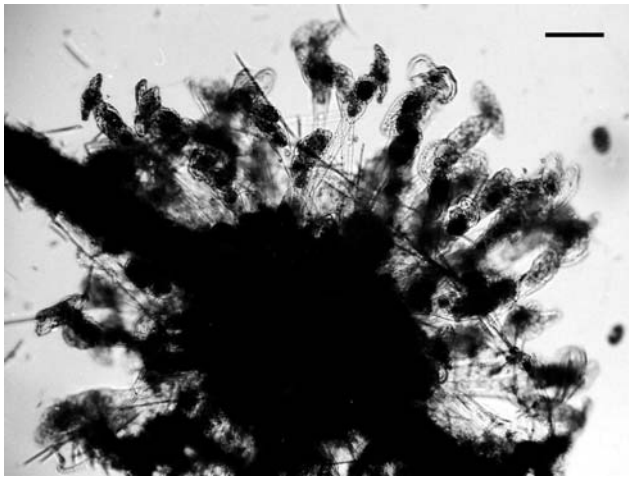


FIGURE 8.33 Flosculariidae: *Lacinularia.* Bar = 250 µm.

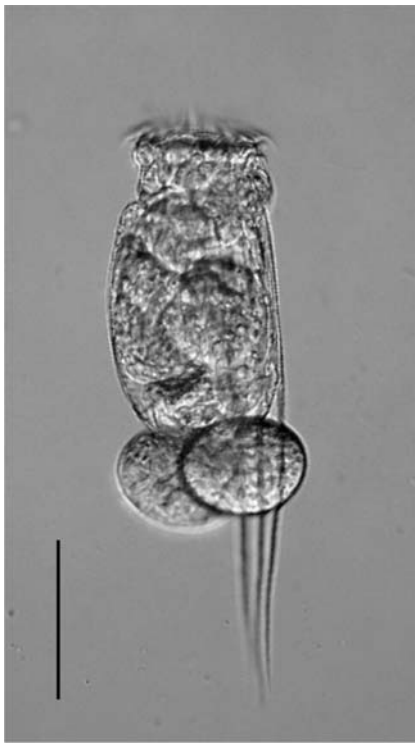


FIGURE 8.34 Flosculariidae: *Filinia.* Bar = 100 µm (PAL). *Photomicrograph courtesy of M.V. Sørensen, University of Copenhagen.*

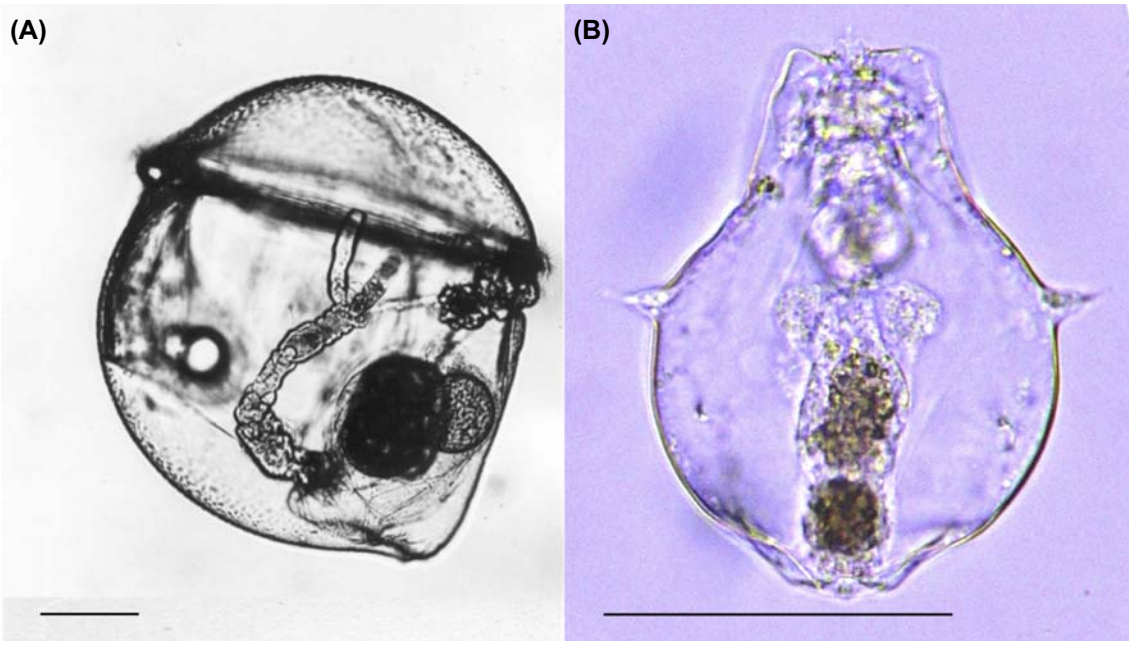


FIGURE 8.35 Trochosphaeridae. (A) *Trochosphaera*. (B) *Horaella.* Bars = 100 µm. *Photomicrographs courtesy of (A) Photomicrograph courtesy of A. K. Gorbunov, The Astrakhanskiy Biosphere Reserve, Astrakhan, Russia; (B) S.S.S. Sarma, Universidad Naćional Autónoma de México Campus Iztacala, México.*



FIGURE 8.36 Testudinellidae: (A) *Testudinella* and (B) *Pompholyx*. (PAL). Bars = 50 µm. *Photomicrograph of Pompholyx courtesy of C. Jersabek, University of Salzburg, Austria.*

Rotifera: Monogononta: Ploima: Families

The separation of two curious congenerics (*Pourriotia*, formerly *Proales*, Proalidae, currently Notommatidae), may be made based on the fact that both are parasitic in galls of the algal genus *Vaucheria*.

1	Rotifers with forcipate trophi (Fig. 13.11j in Volume I)	2
1′	Rotifers with trophi other than above	4
2(1)	Not inhabiting shells of live testate ameba	3
2′	Inhabiting shells of live testate ameba (*Diffugia*); hemiforcipate trophi; consult De Smet (2006) for description and figures	Asciaporrectidae, *Asciaporrecta*
3(2)	Stomach filled with zoochlorellae; gastric glands absent, but with caecae directed toward anterior end; trophi not protrusible; consult De Smet & Pourriot (1997) for details	Ituridae, one genus: *Itura*
3′	Not as above	**Dicranophoridae**
4(1)	Mostly littoral rotifers possessing cardate trophi (Fig. 13.11u in Volume I) having a sucking action or trophi highly modified and stomach with zoochlorellae	5
4′	Rotifers with trophi other than cardate	6
5(4)	Manubria of the trophi with hooks that may be determined in lateral view of the animal (Fig. 13.11u in Volume I); body fusiform, 300–500 µm (Fig. 8.37). Consult Nogrady & Segers (2002) for details	Lindiidae, one genus: *Lindia*

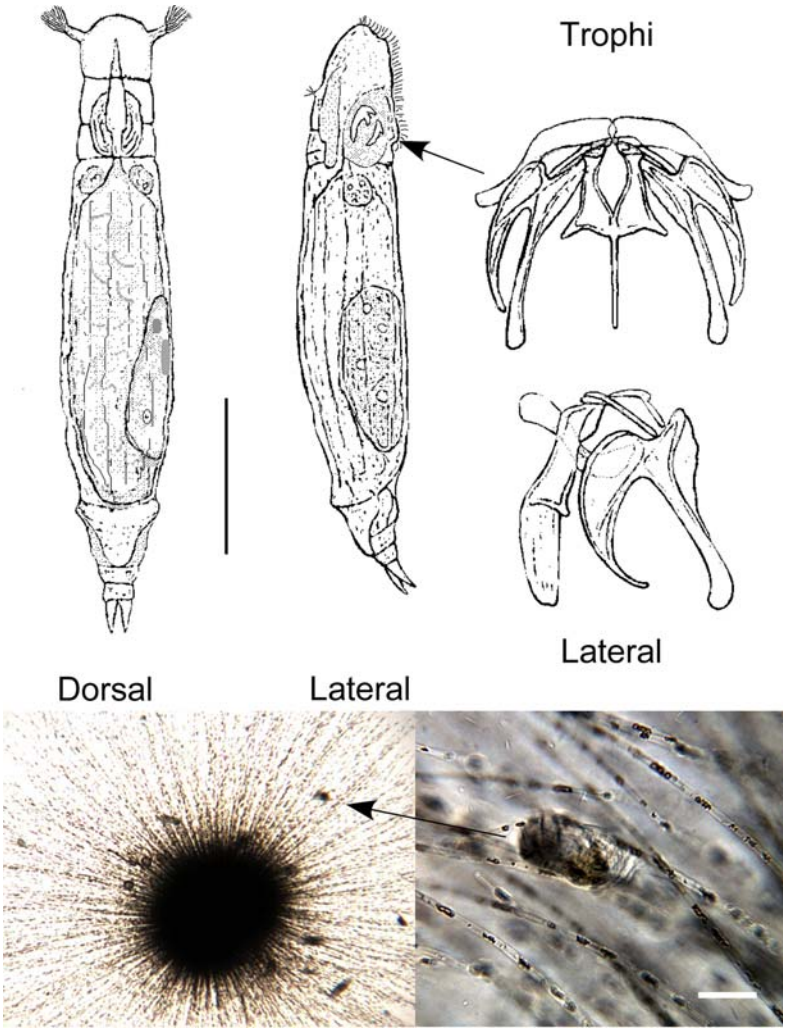


FIGURE 8.37 Lindiidae: *Lindia*. Top panel: left, whole animal; right, trophy. Lower panel: left, animals in a colony of the bluegreen bacteria, *Gloeotrichia*; right, close up. Bar ~100 µm. *Top panel: after Harring and Myers 1922.*

5′	Highly modified trophi, possessing pseudunci, stomach with zoochlorellae, gastric glands absent, a rare littoral, ~275 µm ..... Birgeidae, one species: *Birgea enantia* Harring & Myers, 1922
6(4)	Rotifers not possessing incudate or modified incudate trophi 7
6′	Illoricate, saccate rotifers with modified incudate trophi (Figs. 13.11g, r in volume I) ..... **Asplanchnidae**
7(6)	Rotifers possessing malleate trophi. ..... 8 [In malleate trophi (Figs. 13.11a–c, e, f, p in volume I), each uncus has only 4–7 teeth (unlike the condition found in malleoramate trophi). The fulcrum may be short (malleate) or long (submalleate). In Proalidae the malleate possesses virgate features.]
7′	Rotifers possessing virgate trophi ..... 15 [Virgate trophi are often asymmetrical (Figs. 13.11d, k–o, q, s in Volume I), with a long fulcrum and manubria and generally small rami.]
8(7)	Loricate rotifers: body wall generally thickened and firm 9
8′	Illoricate rotifers: body wall generally not thickened or firm 13
9(8)	Lorica possessing furrows, grooves, or sulci; or with a dorsal, semicircular head shield covering the corona; or with a very strongly developed lorica and a dorsal transverse ridge 10
9′	Lorica lacking furrows, grooves, sulci, or dorsal head shield; without a strongly developed lorica and dorsal transverse ridge 14
10(9)	Lorica lacking medial, ventral furrow or notch, and lacking a head shield 11
10′	Lorica with medial, ventral furrow (but no lateral furrow or grooves) extending the full length of the animal or with a ventral notch in which the foot lies, or with a dorsal, semicircular head shield covering the corona ..... **Lepadellidae**



FIGURE 8.38 Lecanidae: *Lecane*. Bar = 100 µm.



FIGURE 8.39 Scaridiidae: *Scaridium.* Bar = 250 µm (PAL). *Photomicrograph courtesy of M.V. Sørensen, University of Copenhagen.*

11(1)	Lorica not as below 12
11′	Lorica with dorsal, medial sulcus (double keel) or a single dorsal keel ..... **Mytilinidae**
12(11)	Foot usually projecting from between dorsal and ventral plates at the posterior end of the lorica; dorsal and ventral plates separated by a deep furrow or groove ..... **Euchlanidae**
12′	Foot projecting through a foramen (hole) in ventral plate at the posterior end of the lorica; dorsal and ventral plates connected by a weak furrow (groove); ≤200 µm (excluding toes) (Fig. 8.38) ..... Lecanidae, one genus: *Lecane*
13(8)	Mouth set in a large, funnel-shaped buccal field ..... **Epiphanidae** [Some Brachionidae that are weakly loricate will key to here.]
13′	Mouth set in an oblique, ciliated field on ventral side; body swollen, vermiform, or fusiform ..... **Proalidae**
14(9)	Lorica extending beyond body to head, foot, and toes ..... **Trichotriidae**
14′	Lorica not extending beyond body ..... **Brachionidae** [Some Brachionidae that are weakly loricate will key with Epiphanidae.]
15(7)	Body not twisted as a partial helix and/or trophi not asymmetrical 16
15′	Body twisted as a partial helix (asymmetrical) and/or trophi asymmetrical **OR** small, saccate animals, present within the colonial alga *Volvox* where they feed from the inside on the algal cells ..... **Trichocercidae**
16(15)	Not as below 17
16′	Unci tips pointed outwards, capable of protruding through the mouth; body elongate; head with two pairs of lateral lobes; corona stiff, with preoral setae; foot with prominent muscles, foot and toes longer than rest of body; ≤450 µm (Fig. 8.39); consult Nogrady et al. (1995) for details ..... Scaridiidae, one genus: *Scaridium*
17(16)	Not as below 18
17′	Body fusiform; long, knobbed, lateral antennae located near the base of the foot and with long setae; stomach separated from intestine by a circle of bulbous glands; ≤1000 µm (acid waters with a pH < 6.0) (Fig. 8.40) ..... Tetrasiphonidae, one species; *Tetrasiphon hydrocora* Ehrenberg, 1840

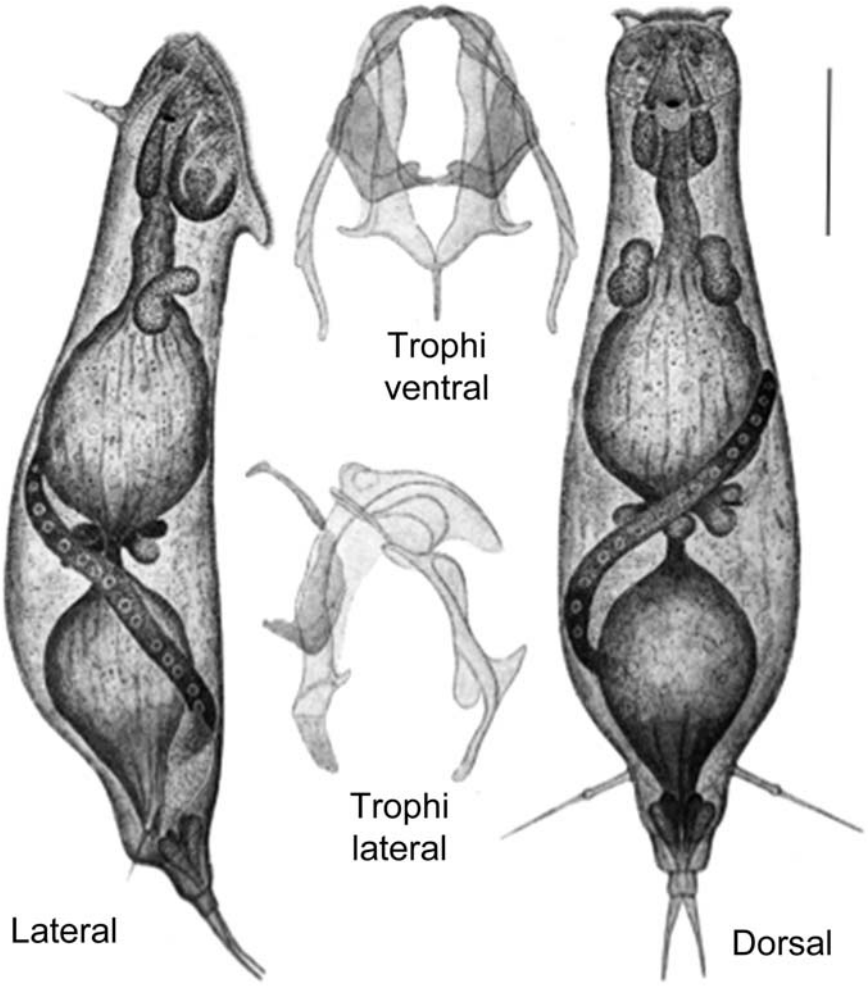


FIGURE 8.40 Tetrasiphonidae: *Tetrasiphon hydrocora.* Bar = 100 µm. *After Harring and Myers 1922.*

18(17)	Not as below 19
18′	Purple plates positioned anterior to the mastax; corona wide, flat, and somewhat circular; foot jointed and long, about half of the total length of the animal, one toe; uncommon, mostly littoral, may be present in plankton samples). Consult Nogrady and Segers (2002) for details, 100−200 µm (Fig. 8.41) ..... Microcodidae, one species; *Microcodon clavus* Ehrenberg, 1830
19(18)	Not as above 20
19′	Small, ovate to saccate; often colored and somewhat laterally compressed; planktonic. Consult Nogrady and Segers (2002) for details ..... **Gastropodidae**
20 (19′)	Illoricate; corona as a circumapical ciliated band with conspicuous auriciform structures (auricles) possessing swimming cilia; apical field with four prominent setae (sensory bristles) foot rudimentary or present (retractable); OR illoricate; corona flat with a circumapical band of swimming cilia; possessing four groups of movable, flattened, sword to feather-shaped appendages (blades, paddles, fins); foot absent; **OR** loricate, sculptured having ridges, grooves, or areolations; corona a simple ciliated band with two digitiform appendages; foot annulated with two toes; **OR** loricate, covered by circular plaques; corona with protuberances next to mouth; foot with two sections. Consult Nogrady & Segers (2002) for details ..... **Synchaetidae**
20′	Animals not as above ..... **Notommatidae**

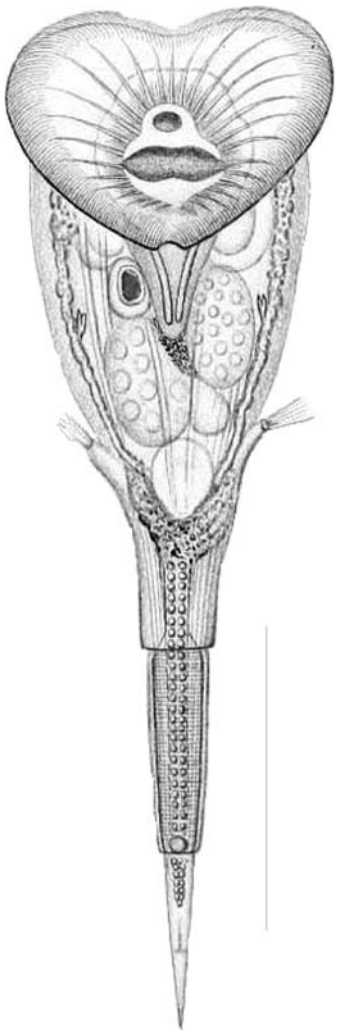


FIGURE 8.41 Microcodidae: *Microcodon clavus*. Bar = 50 µm (PAL). *After Weber 1898.*

Rotifera: Monogononta: Ploima: Dicranophoridae: Genera

Consult De Smet and Pourriot (1997) and Jersabek (1999) for details of the taxonomy. According to De Smet (2006) "... similarities of several ... features of the trophi of Asciaporrectidae, Dicranophoridae, and Ituridae suggest a sister group relationship."

1	Trophi forcipate, rami not bent as below; toes not laterally compressed 2
1′	Trophi modified virgate with rami bent dorsally at 90° midway along their length (partly protrusible and adapted for grasping); epipharynx present; two laterally compressed toes; corona at an oblique angle to body; eyespot absent; illoricate; aquatic mosses and rocks [monospecific; not reported from the Palaearctic] ..... *Dorria dalecarlica* Myers, 1933 [This species has been found among the moss *Fontinalis dalecarlica* and in mountain streams. Additional survey work is warranted.]
2(1)	Corona present although sometimes reduced; mostly free living, but some epizootic or endoparasitic of oligochaetes and slugs 3
2′	Corona absent; endoparasitic in terrestrial oligochaetes, only occasionally free of their host ..... *Balatro*
3(2)	Trophi symmetrical or slightly asymmetrical; teeth on rami often unpaired; unci composed of tooth and shaft 4
3′	Trophi symmetrical or if asymmetrical; unci T-shaped or with three branches 16
4(3)	Incus not Y-shaped; all elements of trophi not rod-like 5
4′	Trophi long and slender; incus Y-shaped; rami and fulcrum long and straight; all elements of trophi as long slender rods (not reported from the Palaearctic) ..... *Streptognatha lepta* Harring & Myers, 1928 [This species has been found among *Sphagnum* moss at low pH (~4.2).]

5(4)	Ramus basal and subbasal chambers not positioned as below; fulcrum plate somewhat rod-shaped 6
5′	Ramus with inner subbasal chamber, with basal chambers situated laterally on external edge of subbasal ones; fulcrum a small triangle or elongated triangle ..... *Dicranophoroides caudatus* (Ehrenberg, 1834)
6(5)	Unci hinged at the posterior end to ramus and manubrium as a three-way joint 7
6′	Unci hinged midway or near tip to middle of tip of ramus, not as a three-way joint 9
7 (6)	Unci not fused; body wall strongly annulated 8
7′	Unci fused to rami at their posterior ends; body wall strongly annulated ..... *Parencentrum* [*Parencentrum* are reported to be more abundant in cold waters. One species of *Encentrum* possessing an annulated body might be confused (see step 13′).]
8(7)	Midway on outer margin of rami, possessing a posteriorly directed projection that ends in a joint connecting uncus and manubrium to ramus; four eyespots without pigment ..... *Myersinella*
8′	Outer margin of rami lacking projections as above, unci and manubrium hinged to corners of rami and bent at right angles near their midpoint ..... *Erignatha*
9(6)	Trophi usually with intramalleus linking manubrium and uncus 10
9′	Trophi usually lacking intramalleus ..... 14 [A few *Encentrum* species lack the intramalleus, a few *Dicranophorus* species possess the intramalleus.]
10(9)	Trunk spines lacking; intramalleus not as a strong inwardly projecting spine 11
10′	Trunk possessing 3–4 pairs of lateral protuberances (hooks) on trunk; intramalleus as a strong spine projecting inwardly, ≤450 µm (Fig. 8.42) ..... *Kostea wockei* (Koste, 1961)
11	Body not as below; foot long or short 12
11′	Body a broad, dorsoventrally flattened oval; foot short ..... *Wigrella*
12 (11)	Body not as below; usually spindle or cylindrical shape, manubria not curved as below 13
12′	Body rounded, bulbous, or saccate and arched dorsally; manubria of trophi crescentiform ..... *Inflatana pomazkovae* Kutikova, 1985 (Lake Baikal)
13(12)	Long foot, >1/5 total body length, toes end in rounded tips. Consult De Smet & Pourriot (1997) for details ..... *Wierzejskiella*



FIGURE 8.42 Dicranophoridae: *Kostea wockei*. *Photomicrographs courtesy of Russ Shiel (University of Adelaide, Australia) and R. Petrie (Murray-Darling Freshwater Research Centre, Australia). Bar c. 100 µm.*

13′	Short foot, <1/5 total body length, toes end in pointed tips. 17
14(9)	Body not pyriform and furrows lacking; teeth on preunci or subunci lacking; body not covered with detritus 15
14′	Body fusiform to pyriform with deep furrows both length- and crosswise; teeth on preunci or subunci present; body wall often covered with detritus; sediment surface and the psammolittoral ..... *Paradicranophorus*
15(14)	Large corona; row of teeth usually present on rami (rarely absent) (Fig. 8.10j in Volume I); usually with two eyespots (frontal); toes long; not endoparasitic ..... *Dicranophorus*
15′	Small corona; teeth absent on rami; toes minute or absent; eyespots lacking; usually endoparasitic in oligochaetes and slugs ... *Albertia*
16(3)	One ramus possessing a large, aliform (quadrate) alula; rudimentary pointed toes, developed as a continuous extension of the foot, lacking a distinct junction (i.e., a yoke-shaped tail appendage) ..... *Pedipartia gracilis* (Myers, 1936)
16′	Alula, if present, rounded, triangular, or hamulate; toes not as above (foot to toe junction present); carnivorous; psammic and among algae and mosses ..... *Aspelta*
17	Trophi not as below ..... *Encentrum*
17′	Unci comprising two, long, thin, acerate teeth, with a small scale like sclerite at a triangular base; cold water species present in glacial lakes >2500 m, central Austrian Alps; c. 200 µm ..... *Glaciera schabetsbergeri* Jersabek, 1999

Rotifera: Monogononta: Ploima: Asplanchnidae: Genera

Consult (Nogrady & Segers, 2002) for details.

1	Animals possessing a foot 2
1′	Animals lacking a foot (one species with a rudimentary foot); intestine and anus absent; 200–2000 µm (Fig. 8.43) ..... *Asplanchna*
2(1)	Animals with complete gut (anus present); 400–700 µm (Fig. 8.44) ..... *Harringia*
2′	Animals with incomplete gut (both intestine and anus absent) (Fig. 8.45) ..... *Asplanchnopus multiceps* (Schrank, 1793)

Rotifera: Monogononta: Ploima: Lepadellidae: Genera

A rare, monospecific genus (*Diplois*), which has been reported from *Sphagnum* bogs in the Palearctic will key here, if its lateral furrows are missed: see Euchlanidae.

1	Head shield poorly developed, retractile 2
1′	Animals possessing a dorsal semicircular head shield covering the corona; 80–225 µm (Fig. 8.46) ..... *Squatinella*
2(1)	Lorica laterally flattened, possessing at least a medial ventral furrow; with or without a sulcus 3
2′	Lorica dorsoventrally flattened, with a deep ventral notch from which the foot extends; ~55–200 µm (Fig. 8.47) ..... *Lepadella*
3(2)	Lorica with a longitudinal dorsal sulcus; foot + toes >½ total animal length; terminal foot segment longer than toes; ~100–160 µm. Compare to *Colurella*; not reported from Palaearctic ..... *Paracolurella*
3′	Lorica lacking dorsal sulcus (continuous); foot + toes <½ total animal length; terminal foot segment less than or equal to toe length; ~50–120 µm (Fig. 8.48) ..... *Colurella*

Rotifera: Monogononta: Ploima: Mytilinidae: Genera

1	Animals with a dorsal longitudinal sulcus (in cross-section appears double keeled); 170–380 µm (Fig. 8.49) ..... *Mytilina*
1′	Animals with a dorsal ridge, but lacking dorsal double keel; 100–250 µm (Fig. 8.50) ..... *Lophocharis*

Rotifera: Monogononta: Ploima: Euchlanidae: Genera

The monospecific genus *Pseudoeuchlanis* has only been recorded from India.

1	Lorica other than pyriform without narrow neck, rather possessing 2–3 plates separated by grooves (sulci); toes not equal in length to body 2
1′	Lorica pyriform with narrow neck, dorsal side swelling into a bulging hump, toes long, about equal to or longer than the body, superficially resembling *Scaridium*, step 58, 420–760 µm (Fig. 8.51) ..... *Beauchampiella eudactylota* (Gosse, 1886)
2(1)	Lorica of two plates, one dorsal and one ventral 3
2′	Lorica of three plates, one ventral, two dorsal separated by sulci (Fig. 8.52) ..... *Diplois daviesiae* Gosse, 1886



FIGURE 8.43 Asplanchnidae: *Asplanchna.* Bar = 100 µm.



FIGURE 8.45 Asplanchnidae: *Asplanchnopus*. Bar = 100 µm.

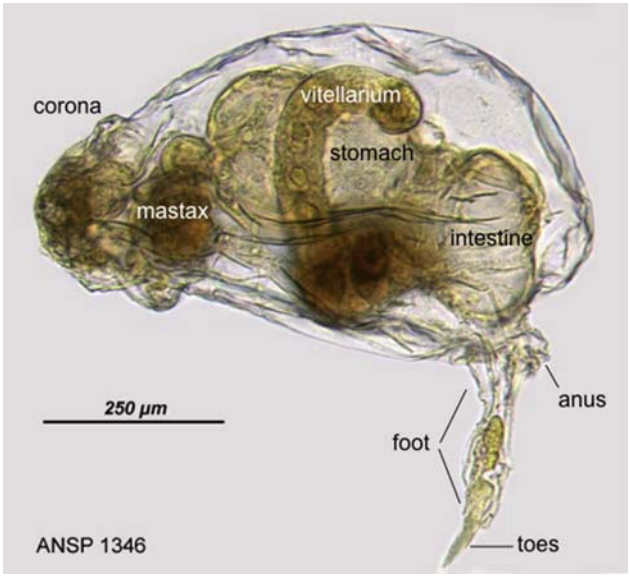


FIGURE 8.44 Asplanchnidae: *Harringia*, left side view. *Photomicrograph courtesy of courtesy of C. Jersabek (University of Salzburg, Austria) and Academy of Natural Sciences of Drexel University. (ANSP = Academy of Natural Sciences of Philadelphia acquisition number.)*

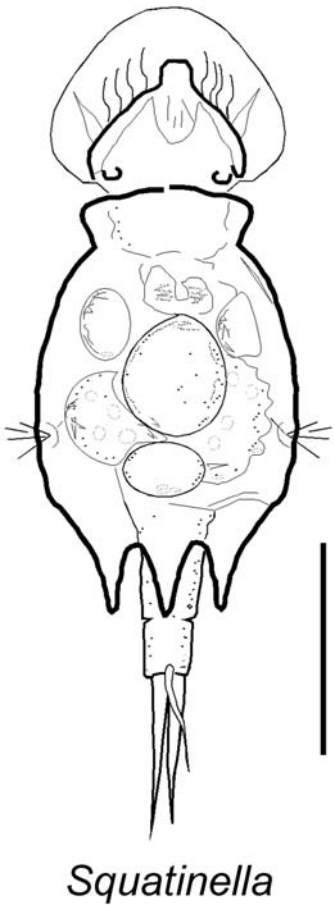


FIGURE 8.46 Lepadellidae: *Squatinella.* Schematic representation from life. Bar ~50 µm.

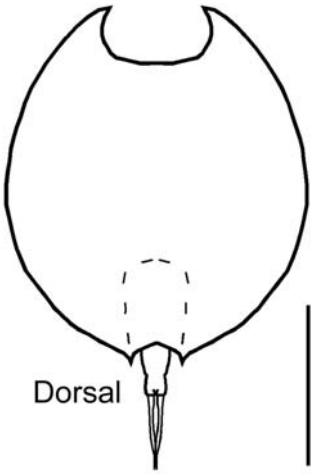


FIGURE 8.47 Lepadellidae: *Lepadella.* Schematic representation from life. Bar = ~50 µm.

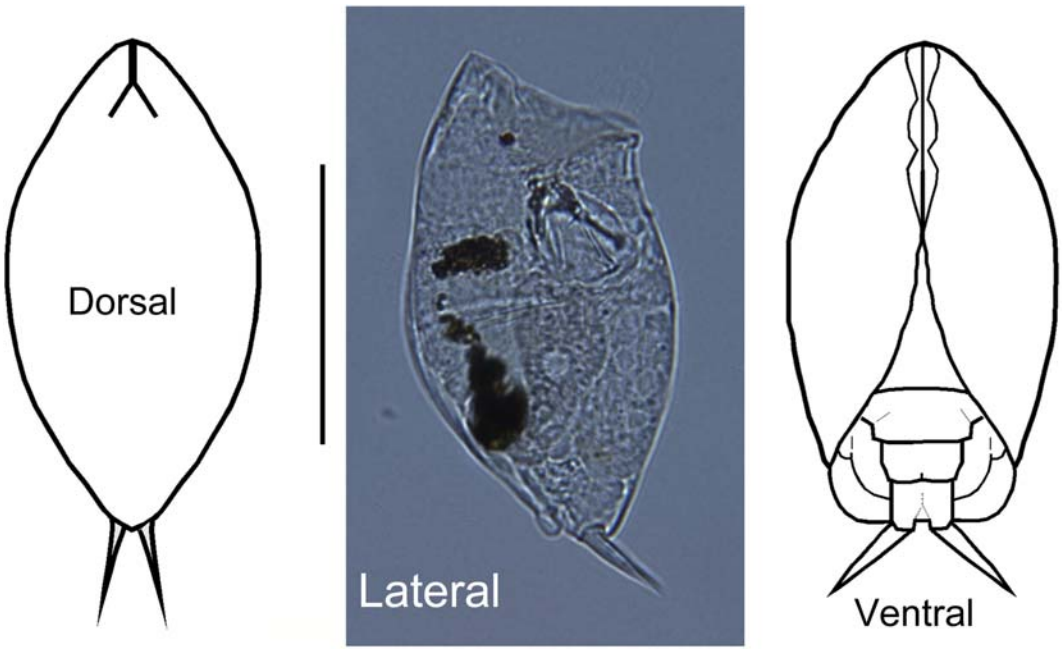


FIGURE 8.48 Lepadellidae: *Colurella.* Schematic representation from life. Bar ~100 µm.

3(2)	Dorsal plate not flat, as least slightly arched; dorsal plate equal to, or wider than, ventral plate 4
3′	Dorsal plate flat, narrower than the slightly arched ventral plate, plates separated by a sulcus around the margin (cf. *Euchlanis* and *Tripleuchlanis*), toes long c. 3/4th body length, ~125–250 µm (including toes) (Fig. 8.53) ..... *Dipleuchlanis*
4(3)	Dorsal plate arched (may be strongly), and indented posteriorly, ventral plate flat, plates separated by a sulcus around margin, foot short with two segments and two, ensiform toes, c. 120–400 µm (Fig. 8.54) (cf. *Dipleuchlanis* and *Tripleuchlanis*) ..... *Euchlanis*
4′	Dorsal and ventral plates slightly arched, the wide marginal sulcus separating plates is divided by a projecting flange producing an extra fold (pleated, accordion-like), foot with three segments, toes shorter than in *Euchlanis* (cf. *Dipleuchlanis* and *Euchlanis*), c. 250 µm (Fig. 8.55) ..... *Tripleuchlanis plicata* (Levander, 1894)

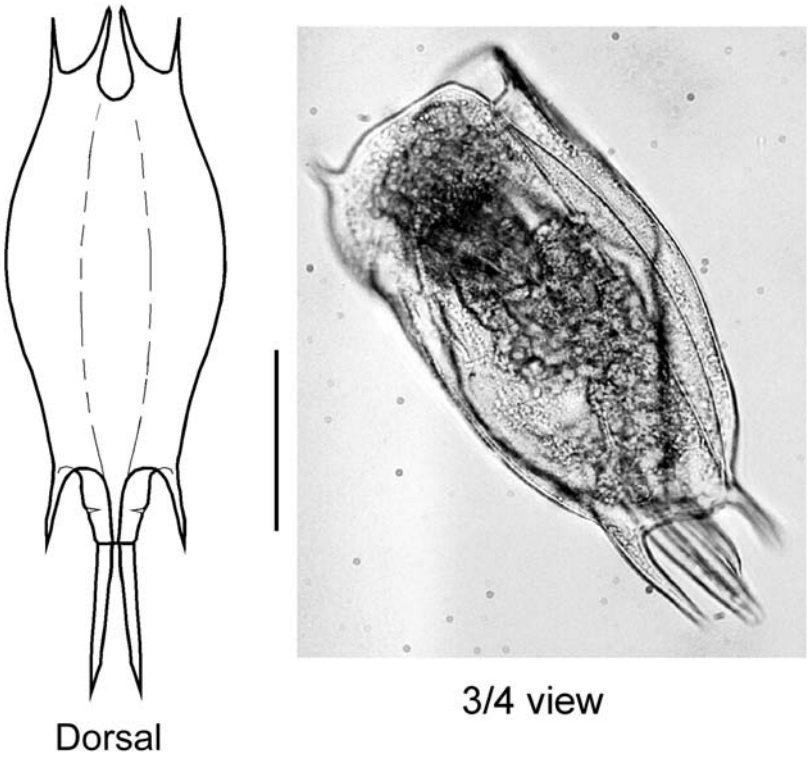


FIGURE 8.49 Mytilinidae: *Mytilina.* Bar = 100 µm.

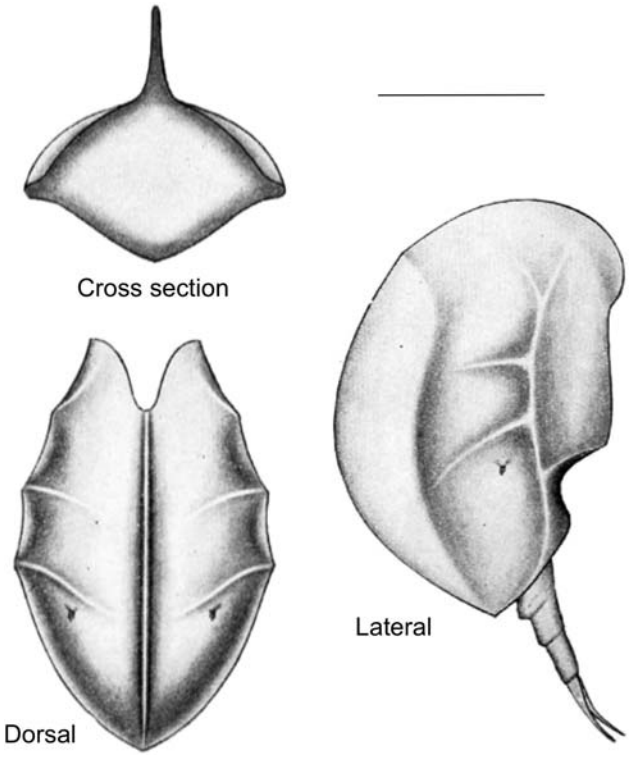


FIGURE 8.50 Mytilinidae: *Lophocharis.* Bar = 100 µm. *After Harring 1916.*

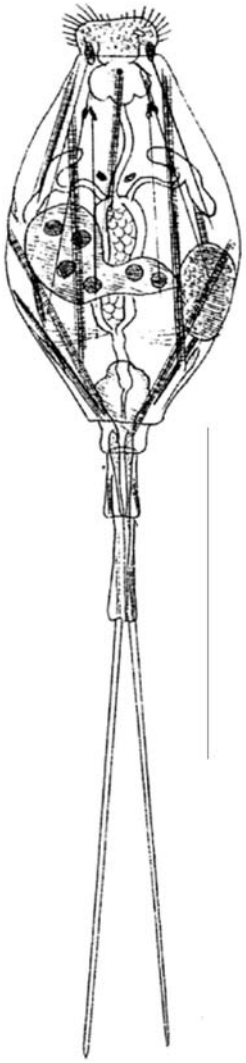


FIGURE 8.51 Euchlanidae: *Beauchampiella eudactylota*. Bar ~250 µm. *After Herrick, 1885.*

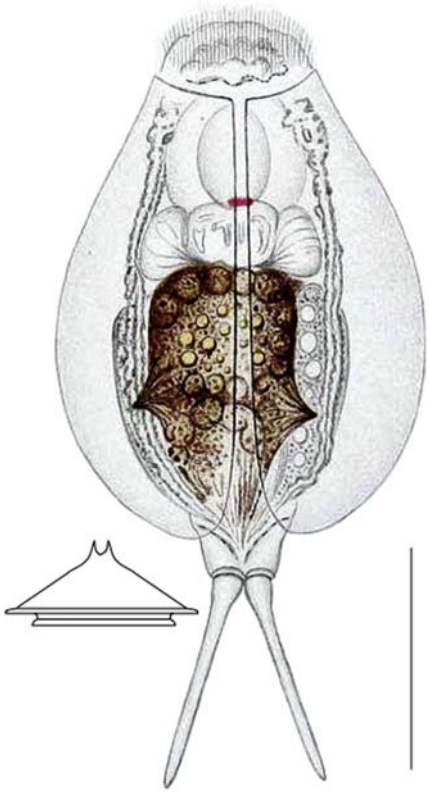


FIGURE 8.52 Euchlanidae: *Diplois daviesiae* Gosse, 1886. Dorsal; Bar ~200 µm. Insert, frontal silhouette. *After Weber, 1898; insert after Hudson and Gosse, 1886.*

Rotifera: Monogononta: Ploima: Epiphanidae: Genera

Some members of the Brachionidae that are weakly loricate may key to the Epiphanidae.

1	Body conical, cylindrical, or saccate, lacking prominent placations or folds 2
1′	Body somewhat quadrate or cylindrical and plicate 4
2(1)	Proboscis lacking 3
2′	Possessing a prominent dorsal proboscis extending from the corona, two eyespots, 200–250 µm (Fig. 8.56); consult Melone (2001) for a review of this genus ..... *Rhinoglena*
3(2)	Body arched dorsally, in lateral view sinuate, tapering to foot with longish toes; 200–350 µm; littoral (Fig. 8.57; trophi: Fig. 13.10 in Volume I) ..... *Cyrtonia tuba* (Ehrenberg 1834)
3′	Body not arched and not sinuate in lateral view; toes short; 200–500 µm (Fig. 8.58) ..... *Epiphanes*
4(1)	Body subquadrate in dorsal view, with a segmented conical foot, possessing a prominent dorsal spur on the last foot joint; dorsal side of the body with a few nearly parallel ridges originating dorsoventrally in the body wall and running laterally to near the corona; 170–250 µm (Fig. 8.59) ..... *Mikrocodides*
4′	Body cylindrical (elongate) lacking a prominent dorsal spur on the last foot joint, possessing prominent transverse folds (plicate) (compare to *Taphrocampa*, step 78), posterior end with short cylindrical structures for egg attachment, 120–135 µm (Fig. 8.60) ..... *Proalides*

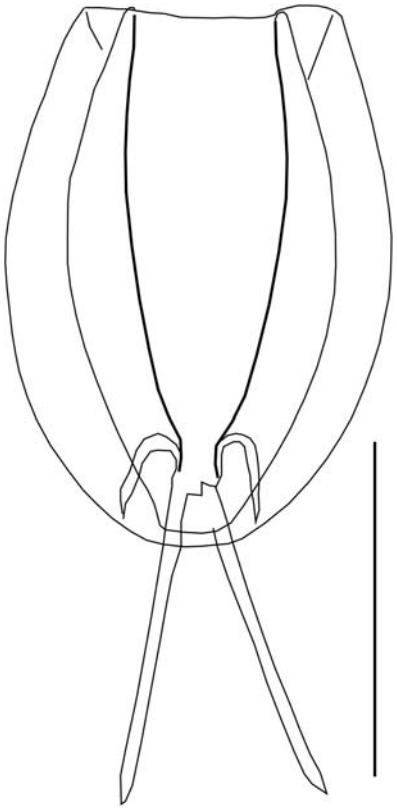


FIGURE 8.53 Euchlanidae: *Dipleuchlanis* (dorsal). (Schematic representation from life.) Bar = 100 µm.

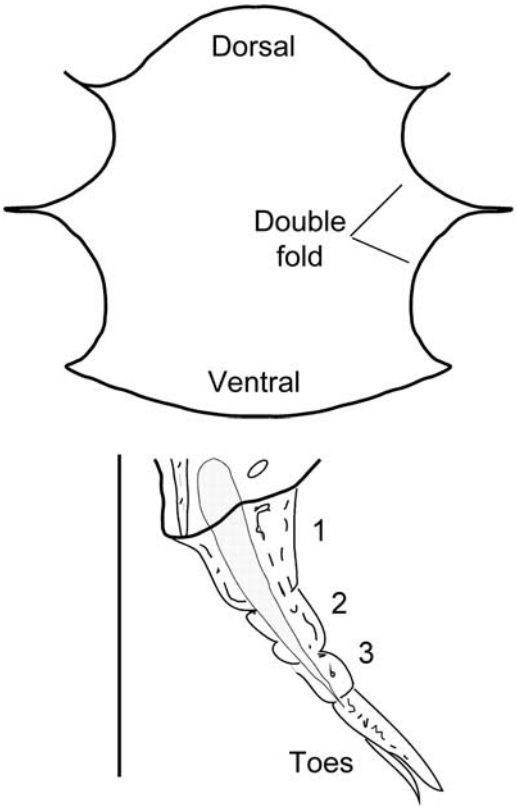


FIGURE 8.55 Euchlanidae: *Tripleuchlanis plicata.* Cross-section (upper); foot, side view (lower). Bar = 100 µm. *After Herrick, 1885.*



FIGURE 8.54 Euchlanidae: *Euchlanis.* Bar = 100 µm.

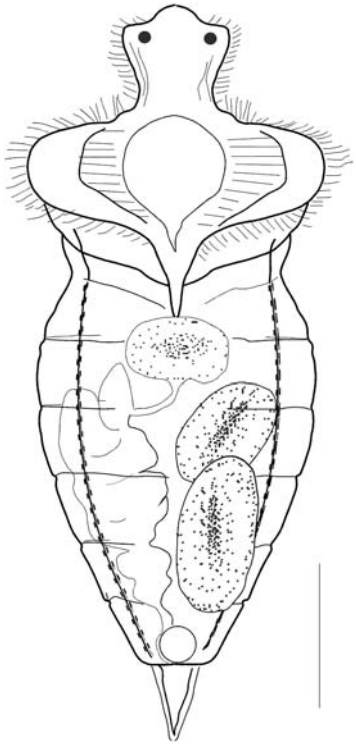


FIGURE 8.56 Epiphanidae: *Rhinoglena.* Ventral view. Bar = 50 µm. *After Hudson, 1869.*

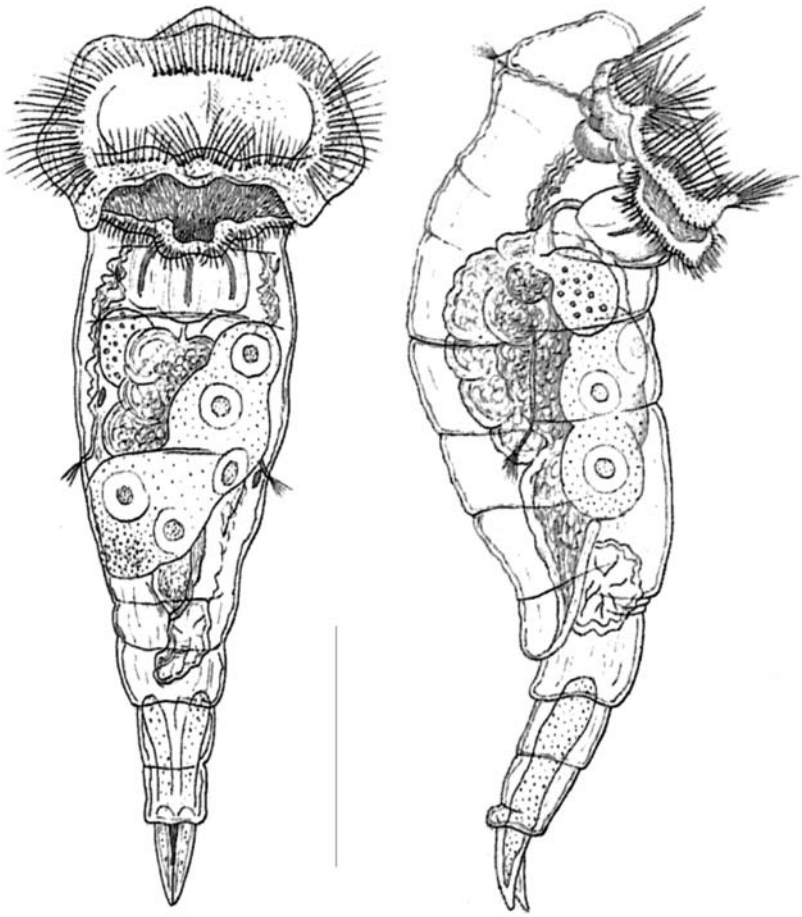


FIGURE 8.57 Epiphanidae: *Cyrtonia tuba*. Ventral (left); left side (right). Bar = 100 µm. *After Hood 1895.*



FIGURE 8.58 Epiphanidae: *Epiphanes*. Bar = 100 µm.

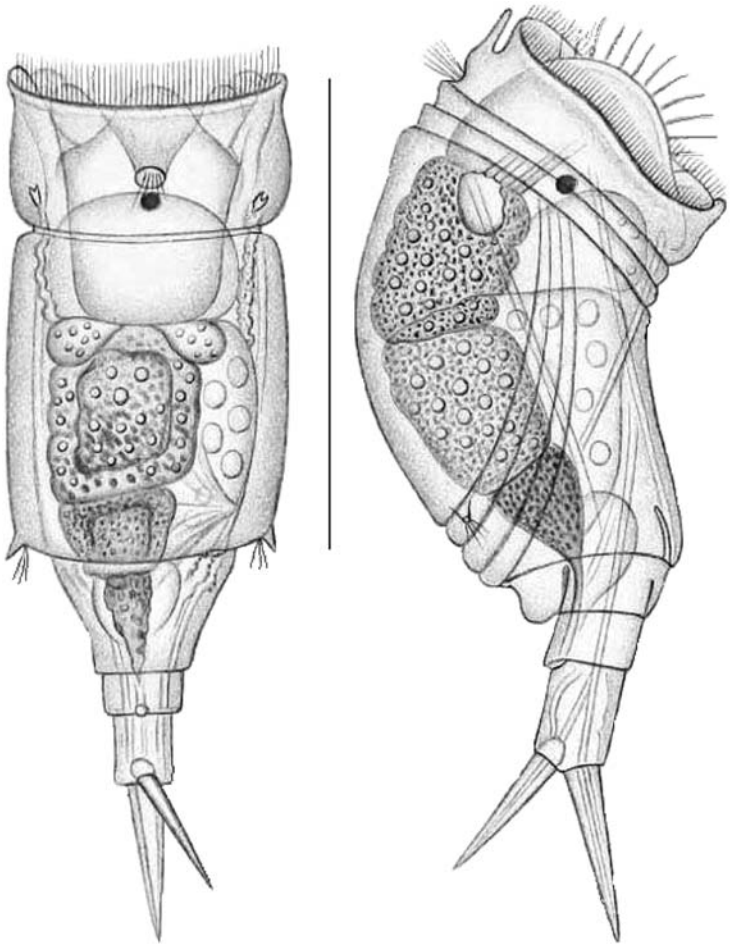


FIGURE 8.59 Epiphanidae: *Mikrocodides*. Arrow = spur. Dorsal (left); side (right). Bar = 100 µm. *After Weber 1998.*

Rotifera: Monogononta: Ploima: Proalidae: Genera

Consult De Smet (1996) for details.

1	Corona lacking cirri; head lacking styli; rostrum lacking or weakly developed 2
1′	Corona possessing long cirri, styli directed posteriorly on both sides of the head, head with rostrum; trophi small, modified malleate ... . *Bryceella*
2(1)	Corona not reduced, cilia not uniformly short, mouth not set posteriorly (set within the buccal field), head separated from trunk, foot not small 3
2′	Simple reduced corona, nearly frontal, covered with short cilia, mostly set posteriorly, head not well separated from trunk, foot small, toes small ..... *Wulfertia ornata* Donner, 1943
3(2)	Tail or foot possessing a papilla with setae or spine, dorsal antennae as a papilla or projection; trophi virgate or malleovirgate *Proalinopsis*
3′	Tail or foot lacking papilla, dorsal antennae not as above ..... *Proales* [*Proales* is a very difficult genus. *Proales daphnicola* Thompson, 1892 is planktonic and may attach to cladocerans. *Proales werneckii* (Ehrenberg, 1834), which is parasitic in galls that it induces in the alga *Vaucheria*, has been moved into *Pourriotia*, Notommatidae. That genus has a second species, *P. carcharodonta*, which also is parasitic in *Vaucheria* (De Smet, 2009a,b).]

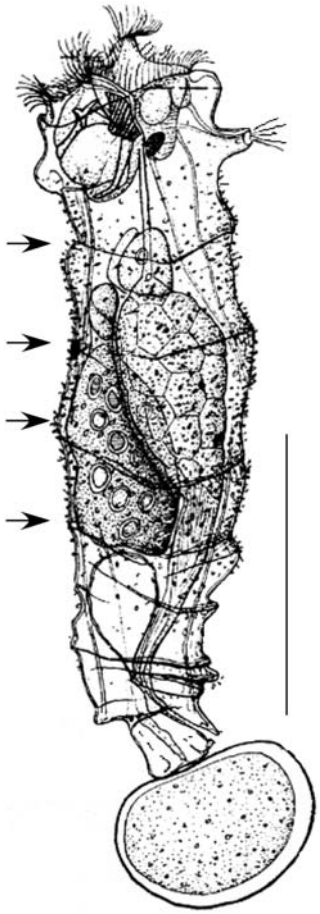


FIGURE 8.60 Epiphanidae: *Proalides tentaculatus.* Bar = 50 µm. Arrows = plications. *After de Beauchamp, 1907.*

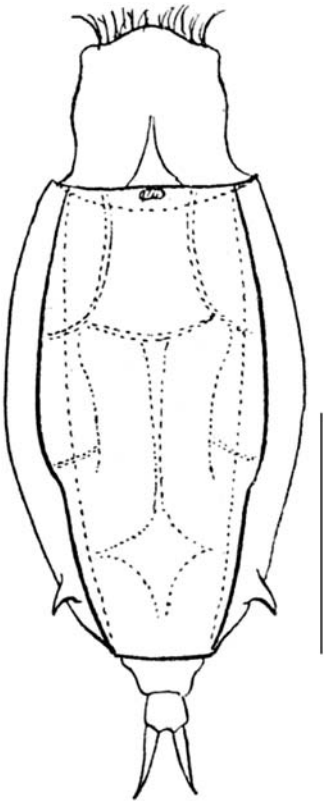


FIGURE 8.61 Trichotriidae: *Wolga spinifera.* Bar = 100 µm. *After Murray, 1913.*

Rotifera: Monogononta: Ploima: Trichotriidae: Genera

Pulchritia (comprising two species) is not included herein as it has been reported from the Palaearctic (Luo & Segers, 2013).

1	Animals with numerous spines on body or with a pair of heavy spines on the dorsal side of the first foot joint	2
1′	Animals lacking numerous spines and lacking spines on the dorsal side of the first foot joint; ~300 µm (Fig. 8.61)	*Wolga spinifera* (Western, 1894)
2(1)	Animals with numerous, long, bilaterally placed spines; 90–250 µm (Fig. 8.62)	*Macrochaetus*
2′	Animals without numerous bilaterally placed spines, but with a pair of heavy spines on the dorsal side of the foot, 200–400 µm (Fig. 8.63)	*Trichotria*

Rotifera: Monogononta: Ploima: Brachionidae: Genera

1	Foot present	2
1′	Foot absent	4
2(1)	Foot jointed, not with morphology or movement as below	3
2′	Foot ringed and capable of movement like a flexible hose, c. 100–400 µm (Fig. 8.64)	*Brachionus*
3(2)	Body in dorsal view more or less box-shaped, ~200 µm (Fig. 8.65)	*Plationus*
3′	Body in dorsal aspect more or less oval-shaped, ~165–350 µm (Fig. 8.66)	*Platyias quadricornis* (Ehrenberg, 1832)
4(1)	Dorsal plate lacking prominent facets	5
4′	Dorsal plate of lorica possessing facets, ~150–450 µm (Fig. 8.67)	*Keratella*

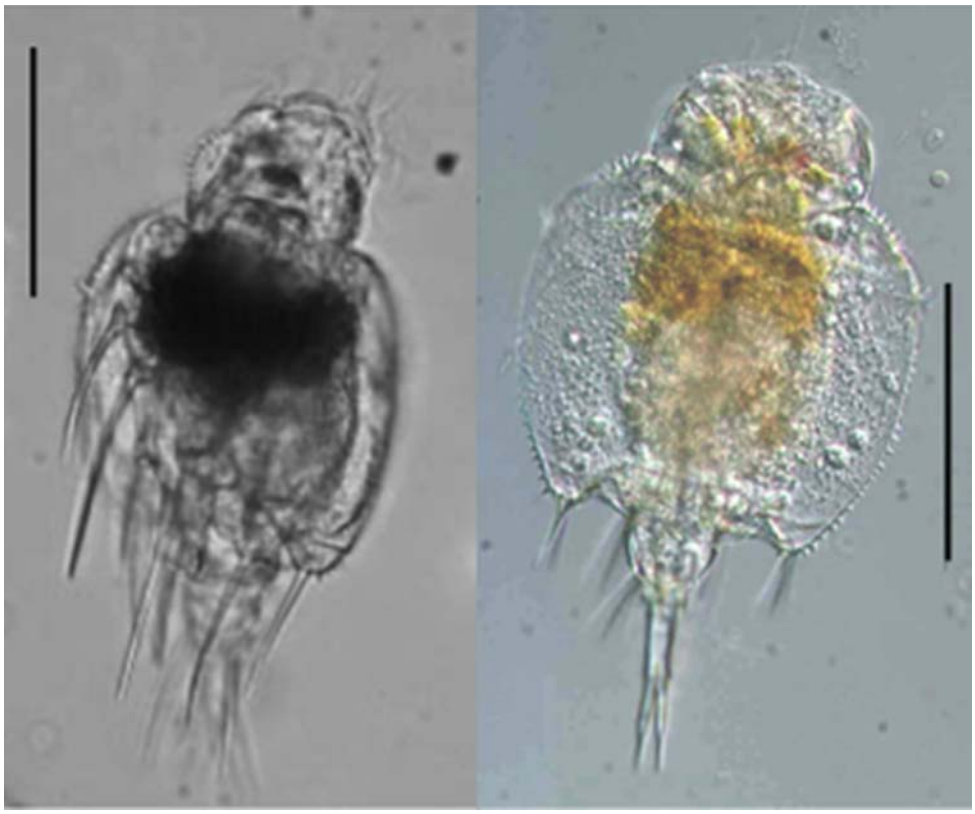


FIGURE 8.62 Trichotriidae: *Macrochaetus.* Bars = 100 µm. *Left photomicrograph courtesy of John Maccagno.*



FIGURE 8.63 Trichotriidae: *Trichotria*. Bar = 100 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso.*



FIGURE 8.64 Brachionidae: *Brachionus*. Bar = 100 µm.

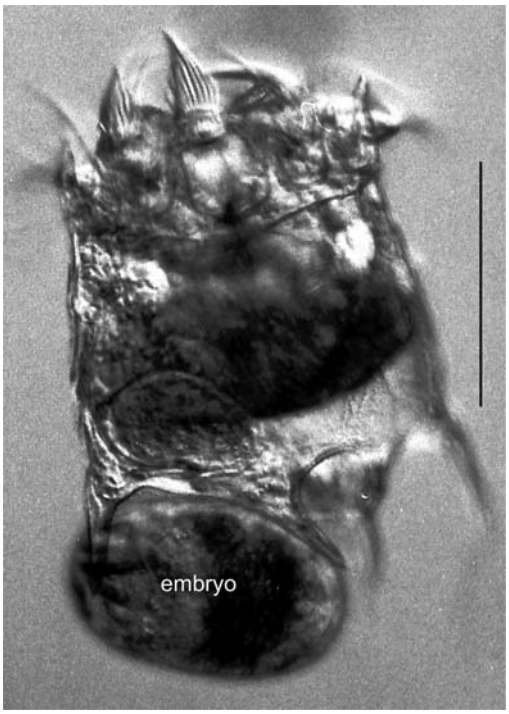


FIGURE 8.65 Brachionidae: *Plationus*. Bar = 100 µm.



FIGURE 8.66 Brachionidae: *Platyias quadricornis*. Bar = 50 µm.

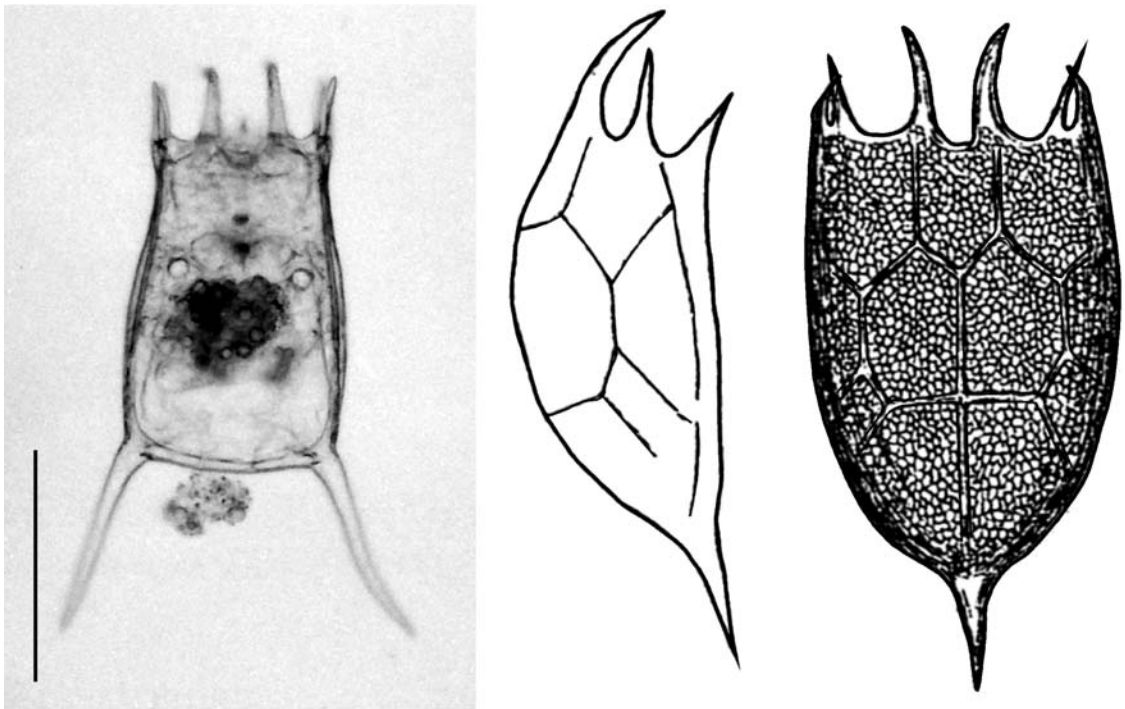


FIGURE 8.67 Brachionidae: *Keratella*. Bar = 100 µm. *Center and left after Lauterborn, 1900.*

5(4)	Possessing symmetrical anterior spines or lacking spines 6
5′	Possessing asymmetrical anterior spines (unequal length), single long, slender posterior spine, c. 100 µm, excluding spines (Fig. 8.68) ..... *Kellicottia*
6(5)	Six anterior spines, dorsal plate with longitudinal striations, anterior margin of ventral plate with scalloping, ≤200 µm (Fig. 8.69) ..... *Notholca*
6′	Lacking anterior spines, dorsal plate arched, ventral plate nearly flat, plates connected by narrow sulci of flexible cuticle, ~100 µm (Fig. 8.70) ..... *Anuraeopsis*

Rotifera: Monogononta: Ploima: Trichocercidae: Genera

1	Body short, not twisted as a partial helix, foot and toes normal 2
1′	Body elongate, loricate, asymmetrical; twisted as a partial helix; toes mostly unequal, spine-shaped; trophi asymmetrical, ~100–500 µm (Fig. 8.71) ..... *Trichocerca*
2(1)	Body showing in cross-section 3–4 lobes (two lateral, one dorsal, one ventral [inconspicuous]), trophi asymmetrical, common in psammon and within of *Sphagnum*, length c. 100 µm (Fig. 8.72) ..... *Elosa*
2′	Body not as above; ~100 µm; lives within *Volvox* feeding on the algal's cells (Fig. 8.73) ..... *Ascomorphella volvocicola* (Plate, 1886)

Rotifera: Monogononta: Ploima: Gastropodidae: Genera

1	Body ovte to saccate; 1–4 dark bodies in stomach (defecation bodies), foot absent, ~75–150 µm (Fig. 8.74) ..... *Ascomorpha*
1′	Body laterally compressed, dark bodies in gut absent, foot present, originating near middle of the ventral side and extending at approximately right angles to the body, c. 80–400 µm (Fig. 8.75) ..... *Gastropus*

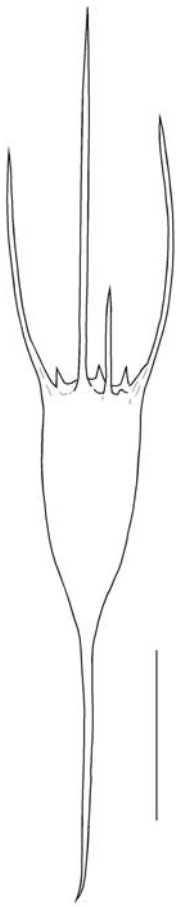


FIGURE 8.68 Brachionidae: *Kellicottia.* Bar = 100 µm. Line drawing from life.

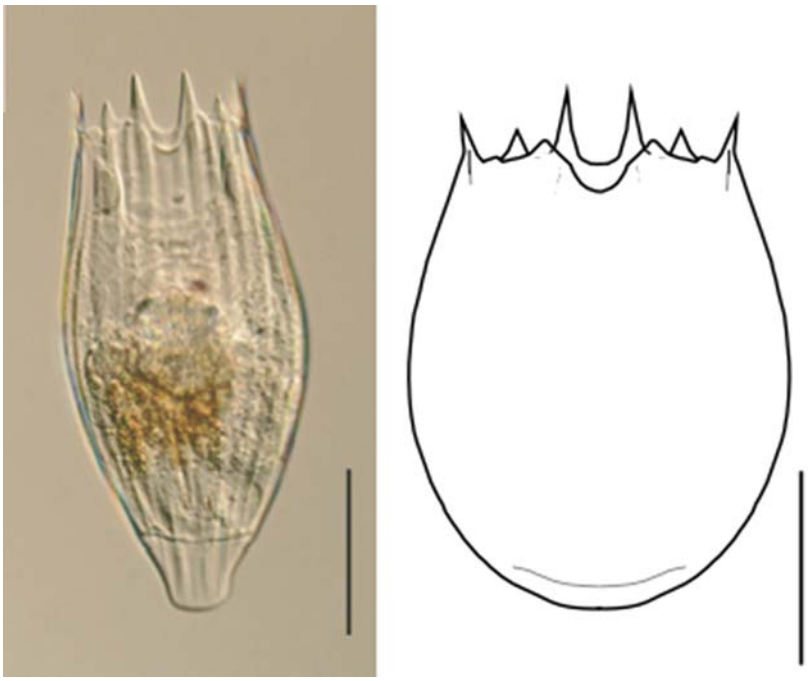


FIGURE 8.69 Brachionidae: *Notholca.* Bars = 50 µm. Line drawing from life.

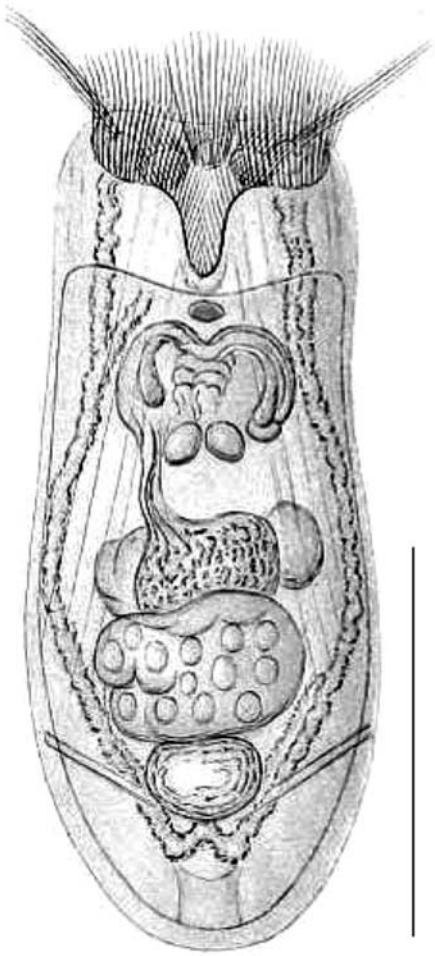


FIGURE 8.70 Brachionidae: *Anuraeopsis.* Bars = 50 µm. *After Gosse, 1851.*

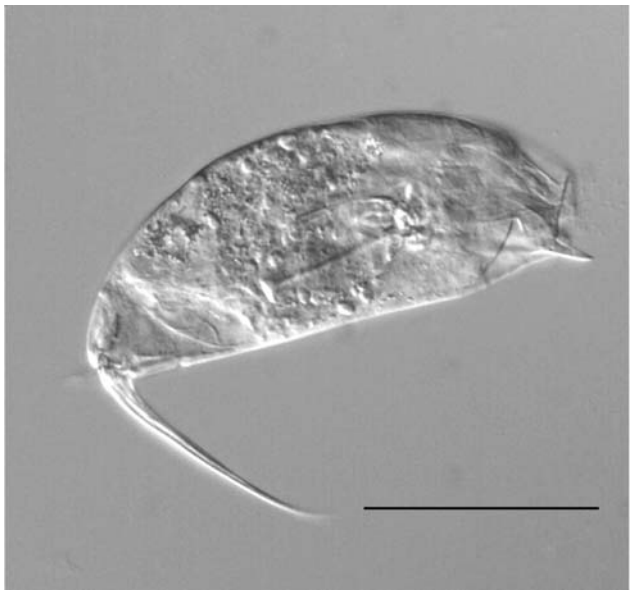


FIGURE 8.71 Trichocercidae: *Trichocera.* Bar = 50 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso.*



FIGURE 8.74 Gastropodidae: *Ascomorpha.* Schematic and photomicrograph. Bar = 100 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso, TX.*

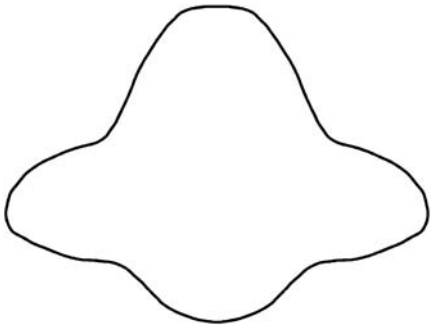


FIGURE 8.72 Trichocercidae: *Elosa*, cross sectional view. Bar = 50 µm. *After Lord, 1891.*

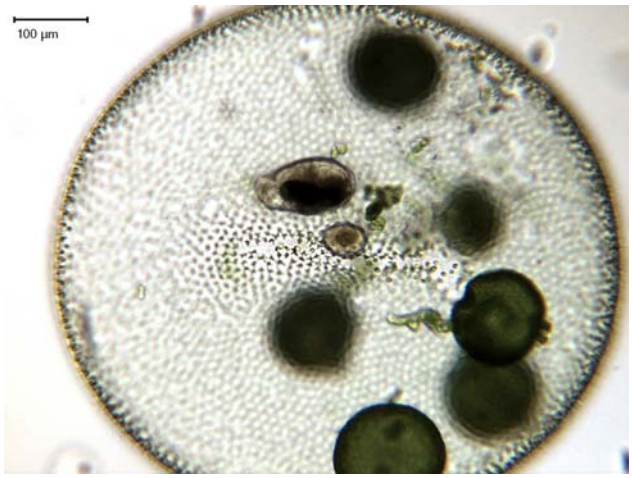


FIGURE 8.73 Trichocercidae: *Ascomorphella volvocicola* preying on cells in the colonial alga *Volvox*. Seen within this colony is an embryo (center) and just above it a female *A. volvocicola* (c. 120 µm). Also present are at least six daughter colonies. This *Volvox* colony has sustained minor damage as evidenced by the line of missing cells along the central portion of the equatorial region and in the upper right quadrant of the parent colony. Some unusual clumps of cells also are seen, one nearby the rotifer and another below and to the right.

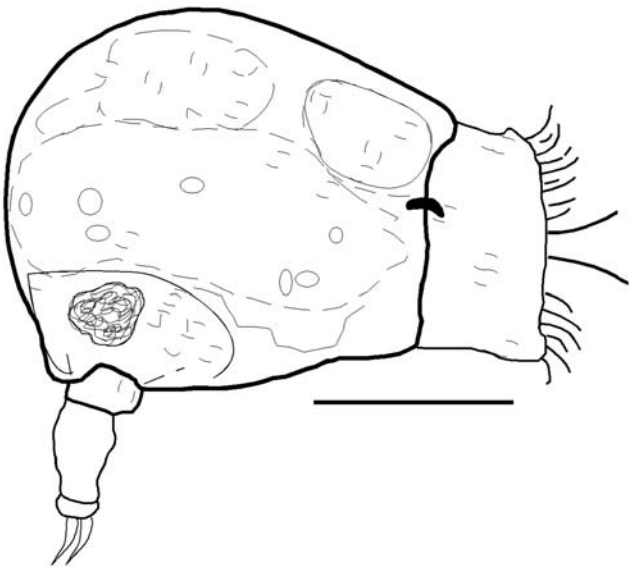


FIGURE 8.75 Gastropodidae: *Gastropus.* Bar = 100 µm. *Drawn from a photomicrograph.*

Rotifera: Monogononta: Ploima: Synchaetidae: Genera

1 Body of animal illoricate 2

1′ Body of animal loricate 3

2(1) Animals with flat, plumiform appendages positioned at the anterior, c. 100–225 µm. (Fig. 8.76) ..... *Polyarthra*

2′ Animals lacking plumiform appendages, head possessing sensory bristles (setae) with a lateral pair of auricles, c. 70–600 µm (Fig. 8.77) ..... *Synchaeta*

3(1) Head shield present, body ornamented with grooves and ridges or reticulate and corona with digiform palps, long flexible foot, c. 130–500 µm (Fig. 8.78) ..... *Ploesoma*

3′ Head shield absent, grooves and ridges reduced or absent; lorica covered by tiny circular plaques; corona without palps, but on either side of the mouth two retractile, cylindrical protuberances, foot short, 150–210 µm (Fig. 8.79); not reported in Palaearctic ..... *Pseudoploesoma formosum* (Myers, 1934)

Rotifera: Monogononta: Ploima: Notommatidae: Genera

Consult Nogrady et al. (1995) for details. Nogrady et al. (1995) defined Notommatidae as "a taxonomically unsatisfactory assemblage of diverse taxa, in need of revision by modern methodology." Given the dearth of competent rotifer taxonomists in the world, we do not see this situation changing in the near future. The following portion of this key covering the Notommatidae is based on Nogrady & Pourriot's remarkable effort in the reference cited above.

1 Not parasitic in the galls of *Vaucheria* 2

1′ Parasitic in galls of *Vaucheria* (Xanthophyceae); ≤ 200 µm. Consult Wallace et al. (2001) and De Smet (2009a,b) for details (Fig. 8.80) ..... *Pourriotia werneckii* (Ehrenberg, 1834)

2(1) Corona not as below 3

2′ Corona a circumapical band of cilia; mouth positioned deeply within a cylindrical snout developed as a suction ring; body slender, fusiform possessing a small conical foot; ectoparasitic on freshwater oligochaetes and leeches ..... *Drilophaga*

3(2) Vitellarium shaped as a ribbon or band 4

3′ Vitellarium reniform or oval 6

4(3) Nuclei within vitellarium arranged linearly 5

4′ Nuclei within vitellarium arranged randomly ..... *Enteroplea lacustris* Ehrenberg, 1830

5(4) Head squarish, not as wide as body; no eyespots; conical foot tapers from body to two tiny toes (genus poorly described) ..... *Pseudoharringia similis* Fadeew, 1925

5′ Head triangular to trapezoidal in shape, wider than body; eyespots on widely separated, small prominences; foot separated from body; toes long; not reported in Palaearctic ..... *Sphyrias lofuana* (Rousselet, 1910)

6(3) Toes much shorter than body length 7

6′ Toes relatively long, mostly longer than body, and unequal in length (except in one species) ..... *Monommata*

7(6) Body not as below; two toes 8

7′ Soft, fusiform body, possessing two lateral humps (retractable); body tapering to conical foot (wrinkled); single conical toe (probably fusion of two); animals always colored (rust to reddish purple) ..... *Tylotrocha monopus* (Jennings, 1894)

8(7) Spine not present as below 9

8′ Small or prominent spine present on the distal end of body or on the distal end of foot 10

9(8) Spine on distal end of body ..... *Dorystoma*

9′ Spine on distal end of foot ..... *Rousseletia corniculata* Harring, 1913

10(8) Body illoricate and not as below 11

10′ Body generally weakly loricate (occasionally illoricate); mostly cylindrical, but shape varies from stubby to fusiform; possessing 3–5 plates separated by sulci (furrows) (Fig. 8.81) ..... *Cephalodella*

11(10) Body wall without spines 12

11′ Body wall possesses rows of small spines ..... *Pleurotrochopsis multispinosa* (Fadeew, 1925)

12(11) Not as below 13

12′ Dorsal side of body with deep plicate folds. (Fig. 8.82) ..... *Taphrocampa*

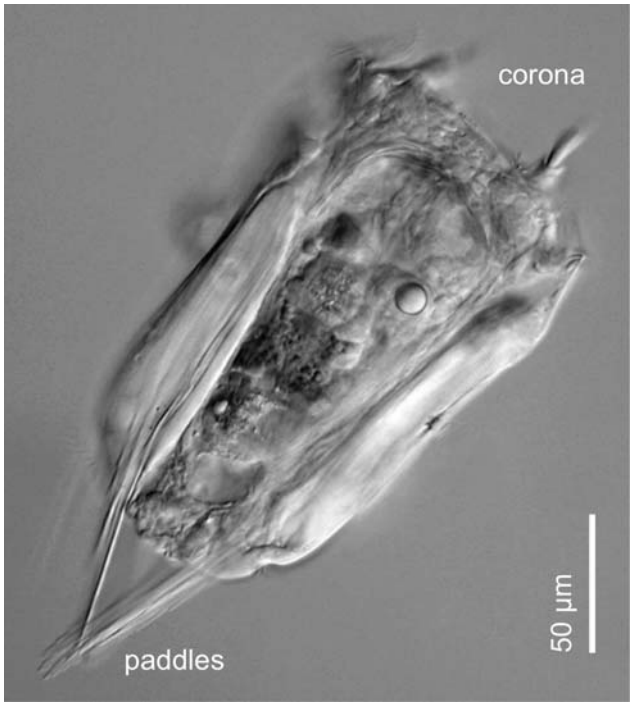


FIGURE 8.76 Synchaetidae: *Polyarthra.* Bar = 50 µm (PAL). *Photomicrograph courtesy of M.V. Sørensen, University of Copenhagen.*

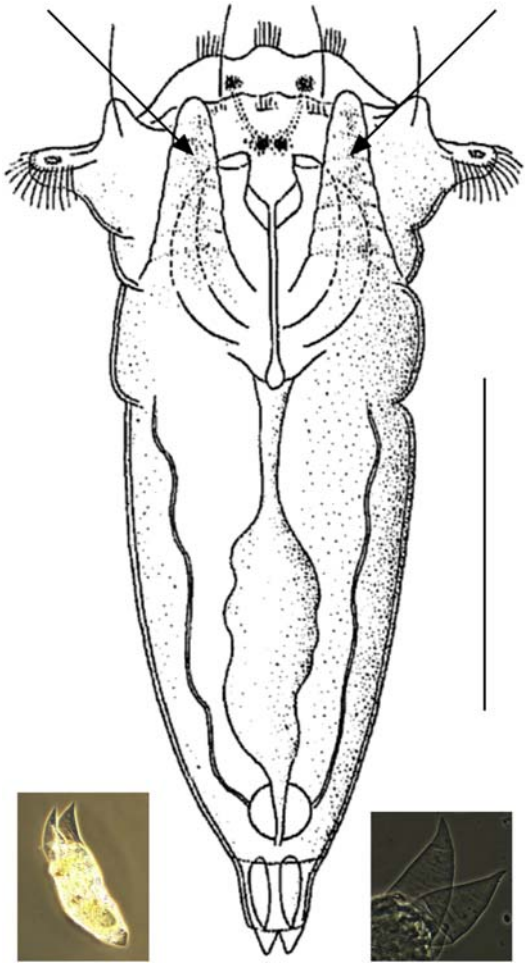


FIGURE 8.77 Synchaetidae: *Synchaeta.* Line drawing of *Synchaeta bicornis*, showing two unusual prominences in this species; inserts preserved samples. Bar = 50 µm. *Line drawing after Smith 1904; inserts courtesy of David Fischer, Cary Institute of Ecosystem Studies, Millbrook, NY.*

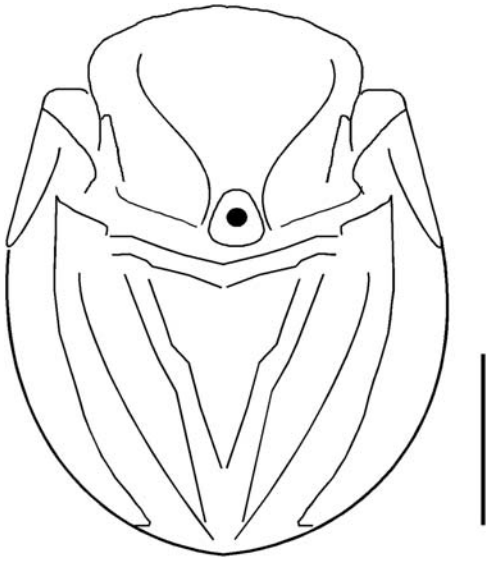


FIGURE 8.78 Synchaetidae: *Ploesoma.* Dorsal view drawn from life. Bar = 100 µm.

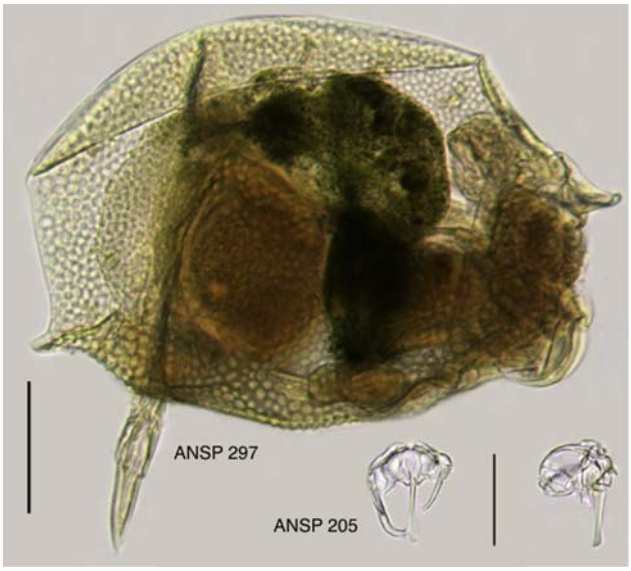


FIGURE 8.79 Synchaetidae: *Pseudoploesoma formosum. Photomicrograph courtesy of courtesy of C. Jersabek (University of Salzburg, Austria) and Academy of Natural Sciences of Drexel University. (ANSP = Academy of Natural Sciences of Philadelphia acquisition numbers.)*

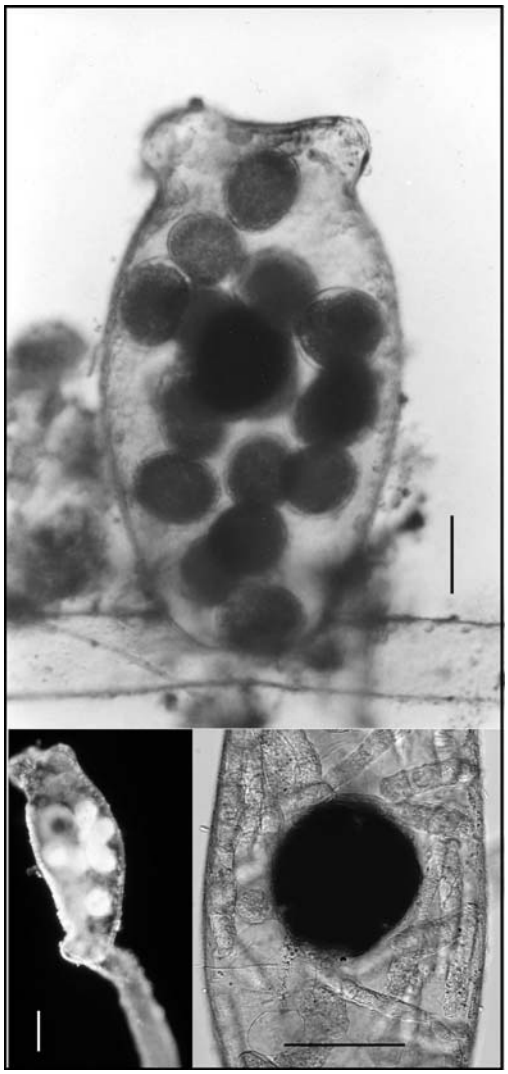


FIGURE 8.80 *Pourriotia (Proales) werneckii.* Bars = 100 µm. Photomicrographs of adult of *P. werneckii* (dark body) with numerous eggs within a gall of *Vaucheria* sp. (upper); parasitized gall (lower left); adult female *P. werneckii* with hatchlings (lower right). *Courtesy of D. Ott, University of Akron, Ohio.*

13(12)	Animals possessing two frontal eyespots	14
13′	Animals lacking frontal eyespots	15
14(13)	Possessing one salivary gland	*Eothinia*
14′	Possessing two salivary glands	*Eosphora*
15(13)	Auricles absent; anterior corona	16
15′	Auricles present (ciliated); ventral corona	*Notommata*
16(15)	Salivary glands are well formed and symmetrical	17
16′	Salivary glands are rudimentary or asymmetrical	*Resticula*
17(16)	Rami triangular (strong, robust).	*Pleurotrocha*
17′	Rami lyrate (curved, thin and slender)	*Pleurata*

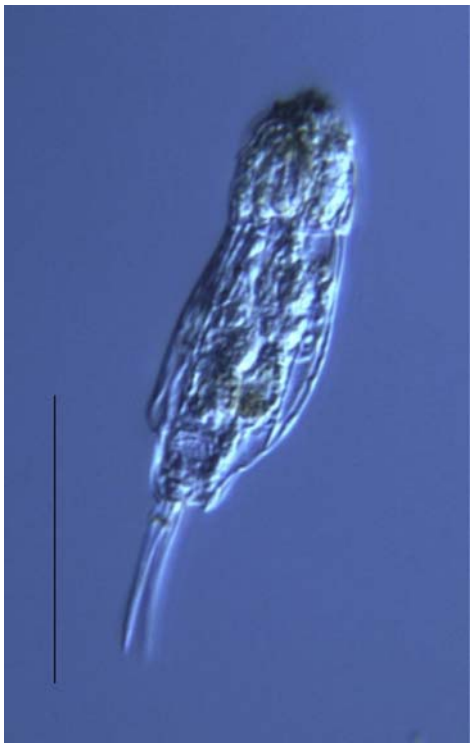


FIGURE 8.81 Notommatidae: *Cephalodella.* Bar = 100 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso, TX.*

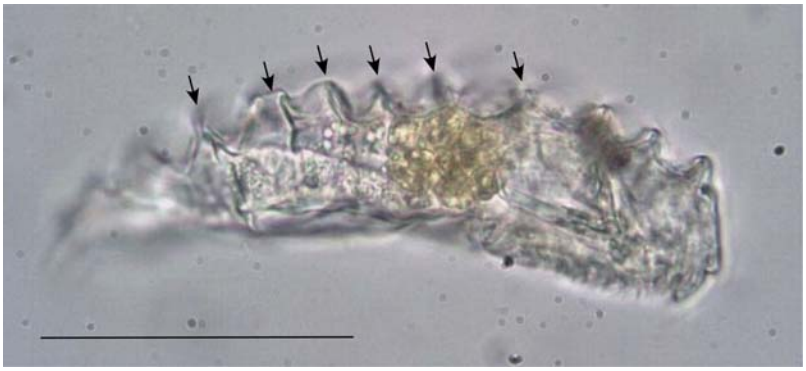


FIGURE 8.82 Notommatidae: *Taphrocampa. Arrows* indicate plication (folds). Bar = 100 µm. *Photomicrograph courtesy of E.J. Walsh, University of Texas at El Paso, TX.*

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Chapter 9

Phylum Nematoda

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INTRODUCTION

Nematodes, or round worms, are small, mostly translucent, nonsegmented worms with a typical filiform body (*nema* = thread in Greek) in 99% of the species. Their largely similar appearance is deceiving since these animals possess amazing plasticity to adapt to a wide range of conditions and habitats. They are either free living or parasites of plants and/or animals and although they occur in almost every habitat (Cobb, 1915), they are essentially aquatic animals. Nematodes depend on moisture for their locomotion and active life but many can survive in an anhydrobiotic state, an adaptation that is common in freshwater nematodes from temporary ponds and polar regions (Womersley & Ching, 1989; Pickup & Rothery, 1991). Nematodes are abundant and functionally diverse, as they feed at all levels of the food web, show various reproductive and survival capacities, and respond in different degree to changes in the ecosystem, such as resource enrichment, pollution, or other kinds of disturbance. Consequently, nematode communities are suitable as bioindicators to assess water quality and environmental changes. In glacier river systems, for example, nematodes develop diverse and abundant populations, which respond to changes in these ecosystems (Eisendle, 2008; Eisendle-Flöckner et al., 2013).

Nematodes, together with the Arthropoda, are classified within the Ecdysozoa [(molting animals), because nematodes in general molt four times during their development resulting in four juvenile stages until the adult stage (Aguinaldo et al., 1997)]. The regulatory neurosecretory control system of molting in both groups shows common features despite their different cuticle composition (Kurzchalia & Ward, 2003).

This review is focused on freshwater nematodes from the Palaearctic region. It does not include nematode parasites of vertebrates living or frequenting freshwater habitats only as eggs or within an intermediate host. The mermithids are insect parasites with different developmental stages (either infective or post-parasitic juveniles); only freshwater adults are treated here and are left at family level. The Mermithida (Mermithidae) in general needs to be revised since many taxa (genera and species) are poorly described and information is missing on aquatic life stages. Many literature resources, often in Russian, are difficult to access and in most freshwater studies, researchers treat them at the family level. Plant parasitic nematode genera associated with submerged aquatic plants or from semi-aquatic habitats and soils have been included although they are not typically freshwater animals.

LIMITATIONS

Despite freshwater nematodes being present in all types of limnetic habitats (including extreme habitats that exclude many other meiobenthic invertebrates) they have received much less attention than terrestrial and marine forms. Their generally small size and the uneven distribution of the few available taxonomists may partly be responsible for the observed bias. Also, information on freshwater nematodes is extremely regionally biased, with limited data from the southern hemisphere. Another factor contributing to the low total number of globally known freshwater nematode species is the relative inaccessibility of taxonomic literature and possible misidentification of many populations or the presence of species complexes (Abebe et al., 2008).

In the last decade, taxonomic studies have developed toward a more integrated approach, combining classical and modern tools and techniques, such as light microscopy, electron-microscopy, and confocal observations with information from molecular analyses (Decraemer & Backeljau, 2015). Free-living aquatic nematodes are usually small (0.2−2 mm long) but the free-living stages of nematodes of aquatic insects such as mermithids are much longer, up to 16 cm.

To study nematodes, specimens have to be fixed and processed for mounting on microscopic slides and observed at high magnification (×1000). Consequently, good fixation is very important for adequate detailed observations (see Material Preparation and Preservation section) and influences appearance, such as resulting in stronger ventral curving of the body and contraction of different structures/organs. Correct use of the microscope, including optimal regulation of the light source, is essential for the

observation of small structures and complex systems in fixed specimens. Making drawings with the use of a *camera lucida* is needed for a better understanding of nematode morphology and functionality instead of observation based on a microphotograph or video capture of a fixed specimen. A combination of methods is recommended, and living specimens provide the most accurate information (Decraemer & Backeljau, 2015).

The main stumbling blocks in nematode taxonomy result from: (1) poor and incomplete species descriptions based on too few specimens, one sex, or juveniles; and (2) lack of detailed illustrations of the holotype and main diagnostic features. They hamper correct morphological and molecular identification (let alone matching molecular and morphological descriptions), and access to type specimens is often not possible. Another important limitation is caused by incorrect interpretation of structures, which obscures correct terminology, as, for example, on the position of the anterior sensilla or the buccal armature (Decraemer & Backeljau, 2015). Often, identification is only possible when both sexes are available or is biased by keys including a mixture of male and female characteristics. Sampling size and extraction methods strongly influence the outcome of a nematode diversity study.

In general, identification keys to higher levels are rare. Subclasses, orders, or suborders appear less clearly defined by synapomorphic features. During evolution, some taxa have lost previously acquired advanced characters or no longer express them phenotypically. However, we have to keep in mind that the main purpose of an identification key is to provide a practical way to arrive at the correct taxon and not to reflect natural phylogenetic relationships.

TERMINOLOGY AND MORPHOLOGY

Nematodes possess an apparently simple and relatively conserved basic body plan that consists of an external cylinder (the body wall) and an internal cylinder (the digestive system) separated by a **pseudocoelomic** body cavity filled with fluid under pressure and containing a number of cells and other organs such as the reproductive system. Freshwater nematodes usually possess a long cylindrical body tapered toward both ends, more pronounced in the tail. Sexual dimorphism can be found, most often in the tail shape (e.g. *Dorylaimus*). Rarely, nematodes show an aberrant appearance as in *Desmoscolex* (Fig. 9.3 A), a largely marine genus with an annulated body covered by main rings composed of secretion and adhered foreign material. Aberrant body shapes often indicate an aberrant locomotion pattern (e.g., *Desmoscolex* sp. show an earthworm-like progress instead of the typical undulating movements in the dorsoventral plane) or even loss of locomotion as in the swollen female of plant-parasitic cyst (*Heterodera*) and root-knot nematodes (*Meloidogyne*). The body **cuticle** may appear smooth (light microscopy), but often shows fine shallow transverse striations or deeper more pronounced annulation and/or longitudinal markings such as **striae** or ridges (Fig. 9.6 C). In many species the cuticular pattern is different at the lateral sides (**lateral fields**), the latter may arise above the body contour and form longitudinal ridges (e.g., *Tylenchida*). More elaborate types of ornamentation can be present, such as punctations (Fig. 9.3 B), spines, setae, papillae, or restricted cuticular differentiations may occur around the vulva, anus, or caudal region in males. **Alae** or wing-like thickening of the body cuticle can be present mainly laterally or sublaterally (e.g., caudal alae in the tail region of the male) and, if well developed, the latter function as a copulatory bursa (Fig. 9.6 I).

The body can hardly be subdivided externally except for the tail region. The mouth is usually anteriorly terminal and a lip or head region may be offset from the rest of the body. The ventral body side can be recognized by the position of the secretory-excretory (SE) pore, the vulva and anus in the female, and the cloacal opening in the male. The nematode body shows two fundamental symmetries: a bilateral and a triradial symmetry (Figs. 9.1 A, B). The terminology for both types of symmetry introduced by Coomans (1978) permits the description of any structure. The bilateral symmetrical body plan applies to all structures, except the **pharynx** (**esophagus**), and divides the body into a dorsal, ventral, and two lateral quadrants. The latter quadrants are subdivided by **mediodorsal, medioventral, and mediolateral radii** in a total of two subdorsal, two subventral, and four sublateral regions (Fig. 9.1 A). The triradially symmetrical body plan only applies to the pharynx (esophagus) and has a dorsal region (larger than in bilateral symmetry) equal in size to two ventrosublateral regions. Because teeth are in general part of the **stegostom** (anterior pharynx), triradial symmetry is applied to them (Fig. 9.1 B). At the anterior end, the bilateral symmetry of the body fuses with the triradial symmetry of the pharynx into a radial (often hexaradial) symmetry (De Coninck, 1942). The primitive pattern of the lip region consists of six separate lips (two subdorsal, two subventral, and two lateral lips), which may fuse partially (*Mononchus*) or completely or in pairs of two (one dorsal, two ventrosublateral). In Tylenchida, the real oral opening may be displaced internally and connected by a **prestoma** to the prestomatal opening. The mouth opening may be differentiated into an oral and/or a labial disc (Fig. 9.3 O). Internally the cephalic region is strengthened by a weak or heavily sclerotized cephalic framework (Fig. 9.2 B). The anterior **sensilla** are arranged in two circlets, each of six labial sensilla, and when six lips are present, each lip bears an inner and an outer sensillum on its radial axis. A third circlet of four cephalic sensilla (CS) is bilaterally arranged in a submedian position, primitively located posterior to the lips as the first in a series of somatic

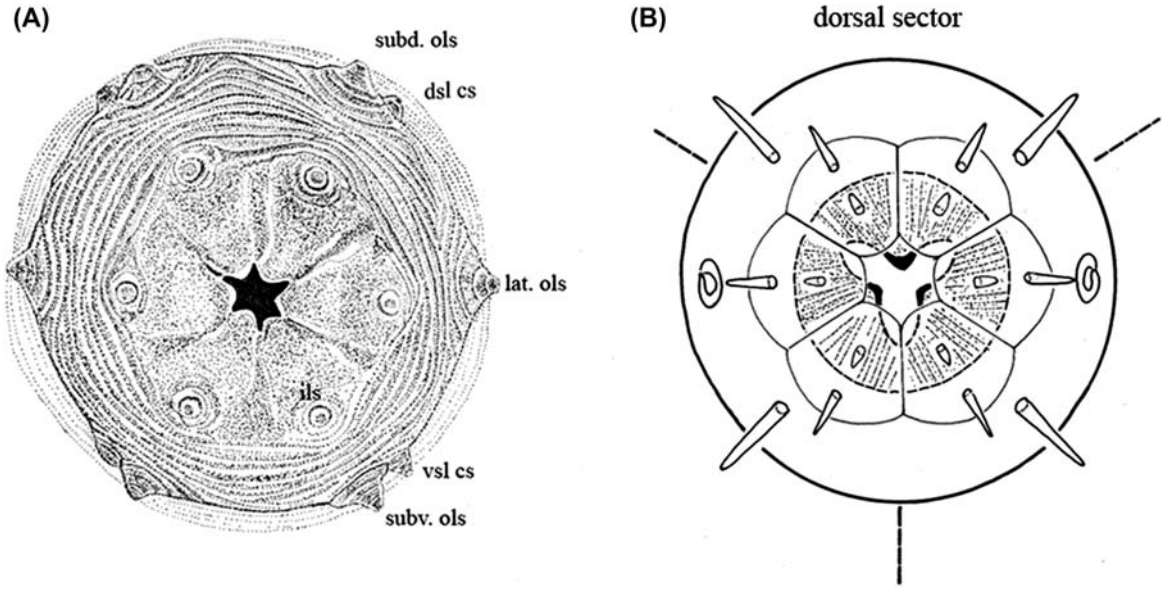


FIGURE 9.1 (A) Front view of a mononchid nematode showing the radial symmetrical arrangement of the labial sensilla and bilateral symmetry of the cephalic sensilla. dsl. cs: dorsolateral cephalic sensillum; lat. ols: lateral outer labial sensillum; subd. ols: subdorsal outer labial sensillum; subv. ols: subventral outer labial sensillum; vls. cs: cephalic seta; and (B) front view showing the triradial symmetry of structures related to the pharynx with a dorsal tooth and two ventrosublateral teeth. *Adapted from De Coninck, 1942.*

setae. This primitive pattern is indicated as $6 + 6 + 4$ (Fig. 9.1 B). In more advanced (apomorphic) patterns one can observe $6 + 10$ (Fig. 9.1 A) or $10 + 6$ when the CS have migrated on the lips (some Actinolaimidae). The anteriormost circlet of inner labial sensilla (ILS) is usually **papilliform**. The second circlet of outer labial sensilla (OLS) and the four cephalic setae are usually **setiform** in aquatic nematodes and papilliform in most other species; anterior labial sensilla can appear absent on the head/lip surface due to receptors ending beneath the cuticular surface. In addition, there is a pair of large chemoreceptors, the amphids (Fig. 9.3), considered to be the most complex sensilla at the anterior end and located laterally and postlabially in the basic pattern. In light microscopy, we most easily observe the most distal amphidial part, the **fovea**, either as an external excavation (Fig. 9.3 K) in the cephalic

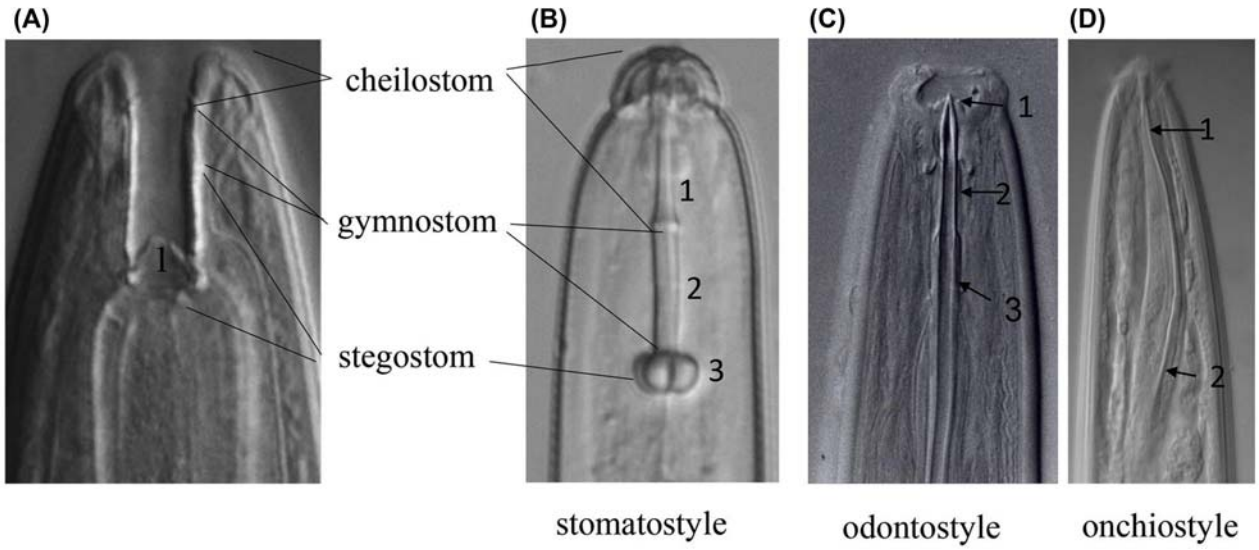


FIGURE 9.2 Structure of the buccal cavity with different types of feeding apparatus: (A) teeth: glottoid apparatus in *Caenorhabditis*; (B) *Scutellonema*, 1: cone, 2: shaft, 3: knobs; (C) *Paractinolaimus*, 1: onchia, 2: odontostyle, 3: odontophore; and (D) *Trichodorus*, 1: onchium, 2: onchiophore. *(B)Ccourtesy of S. Subbotin.*

cuticle (often wrongly referred to as the amphid or aperture) or an invagination of the cuticle often forming a typical inner pocket connected to the exterior through a slit-like amphidial aperture (Figs. 9.3 E, G); the fovea can be filled with a gelatinous matrix (*corpus gelatum*) secreted by the sheath cell. The fovea is connected to the **amphidial duct** through a duct pore; the duct ends in the **fusus** (also called **amphidial pouch**). The amphidial foveae appear quite variable according to the taxa. In Enoplia and Dorylaimia, the fovea typically forms an invaginated pocket. In Chromadoria, the variation in fovea shape is most obvious (e.g., from circular, oval, mono- or multispiral, elongated, or looped) while in many Tylenchida the amphidial fovea is very small and may even be absent; the duct pore becomes the external opening and has migrated onto the lip area and become obscure in light microscopic observation (Fig. 9.3 O). The fovea may show sexual dimorphism. Somatic sense organs occur in longitudinal rows along the body; they may connect with the outside through pores, papillae, or setae and are often associated with glands. Specialized forms are **deirids**, paired lateral sense organs; phasmids, usually laterally on the tail and connected to the environment by a small pore [large phasmids are described as **scutella** (Fig. 9.6 H)]. In a number of aquatic nematodes special filiform somatic sense organs located laterally in the epidermis are described as metanemes; they are well developed in *Tobrilus*.

The wide diversity of food sources and methods of food intake is reflected in the diversity of the structure of the digestive system, especially of stoma and pharynx. The digestive system consists of three main parts: (1) the **stomodeum** (foregut) comprising the buccal cavity or **stoma** (=stoma *sensu lato*) composed of the cheilostom (mouth cavity) and the pharyngostome (with anterior **gymnostom** secreted by arcade cells and not surrounded by pharyngeal tissues and **stegostom** secreted by pharyngeal epithelium); (2) the **mesenteron** (intestine or midgut), and; (3) the **proctodeum** (rectum or hindgut). The **cheilostom** is lined by invaginated body cuticle that can be more or less sclerotized, supported by either bacilliform thickenings (**cheilorhabdia**). In Chromadorina, cheilorhabdia form a crown with 12 points or "pearls" supporting the lip region; the latter represents an important diagnostic character of the suborder. The **pharyngostom** is the anteriormost part of the pharynx and follows the triradial symmetry. It varies in shape and structure as well as in the presence or absence of a stylet, tooth/teeth, mandibles, and denticles (Fig. 9.4). Teeth are present in many taxa and implanted on a movable or solid base in the **metastegostom**, with or without specialized structures such as apodemes (Fig. 9.5 M) for insertion of associated muscles; teeth may be solid or hollow, equal in size or different in size, whereby usually the dorsal tooth is the largest, but also the left or right ventrosublateral tooth can be the largest one. During evolution, a specialized aciculate tooth has evolved to a hollow tube (**odontostyle**) as in predacious and plant parasitic dorylaims (Fig. 9.2 C); it is inserted on a more or less modified part of the pharyngeal wall, functioning as a support or odontophore. Another type of hollow stylet, the **stomatostyle** (Fig. 9.2 B), originates in situ and is characteristic for Tylenchida, Aphelenchida, and Aphelenchoididae. A third type of stylet (**onchiostyle**) as found in the plant ectoparasitic Trichodoridae is in reality an aciculate tooth (**onchium**) on a support (onchiophore) formed by a thickening of the dorsal lumen wall of the pharynx (Fig. 9.2 D).

Wieser (1953) was the first to develop a classification of feeding types for free-living aquatic nematodes based on the size of the buccal cavity and the absence or presence of teeth and their size: 1A, selective deposit feeders with minute buccal cavity without teeth; 1B, nonselective deposit feeders with buccal cavity conical or wide cylindrical without teeth; 2A, selective epistratum feeders with small buccal cavity with small teeth; and 2B, carnivores with large buccal cavity with large teeth. Other classifications considered also behavioral features and distinguished, for example, aquatic freshwater nematodes that are deposit feeders or swallowers [no teeth, e.g., *Daptonema*, *Plectus* (Fig. 9.4 M)], epistrate feeders (small tooth, e.g., *Punctodora*), suctions feeders (with stylet, e.g., *Dorylaimus*), or chewers (large stoma with one or more teeth, such as *Prionchulus*) (Moens et al., 2006).

The nematode pharynx (esophagus) is a muscular as well as a glandular organ and varies in structure and function according to the taxa. The simplest type is a cylindrical tube (Fig. 9.5 A) between the buccal cavity and intestine. A more complex pharynx is subdivided in two (**corpus**, **postcorpus**; Fig. 9.5 C) or three different parts (corpus, **isthmus**, and **terminal bulb**; the latter two form the postcorpus). Such a complex pharynx can be shorter than a cylindrical one through the division of labor. Species consuming liquid food such as plant parasites have a median bulb (=**metacorpus**) derived from the posterior part of the corpus; the metacorpus contains a valve and strong musculature (Fig. 9.5 E), which allows for stronger suction (Decraemer et al., 2014). Bacterial feeders often have a **valvular apparatus** in the terminal bulb (Figs. 9.5 H, I). The pharyngeal lumen is triradiate, lined with cuticle. At the level of the corpus, the three lumen radii (one dorsal and two dorsolateral) terminate in radial tubes in Plectoidea and Rhabditida. The pharynx also contains gland cells, the number of which differs between taxa. There are usually three unicellular glands as, for example, in many Tylenchida or five unicellular glands (one dorsal and two ventrosublateral pairs) as in rhabditids or dorylaims (except three in longidorids). The position of the outlet of the dorsal pharyngeal gland is of taxonomic importance and differentiates the Aphelenchoidea (where the outlet is in the

metacorpus) from the other taxa of the Tylenchida, with the outlet in the procorpus, often close to the stylet base. In Dorylaimida, all outlets of all five pharyngeal glands are located posterior to the nerve ring (Fig. 9.5 D). In exceptional cases, as in Mermithidae, the pharynx separates from the intestine during development and becomes a series of gland cells or **stichosome**. The **cardia** or pharyngo-intestinal junction is the posteriormost part of the stomodeum. Typically, it is a one-way valve that prevents regurgitation of food in the intestine into the pharynx. In a number of genera, three unicellular glandular cells may be present around the valves. In general, the cardia is of restricted diagnostic value except in the Mononchida, where the presence of a **tuberculate cardia** is a derived character (synapomorphy) for the suborder Anatonchina (Figs. 9.4 D, E). The intestine is a straight tube, entirely endodermal in origin. The intestine is generally divided into three parts which are seldom recognizable in total mounts except for the posterior **prerectum** with long microvilli (e.g., Dorylaimida). In mermithids, the intestinal connection with both the pharynx and anus is lost and a food storage organ or **trophosome** occurs. The rectum (**proctodeum**), a posterior ectodermal part, is connected to the intestine through a valve surrounded by a sphincter muscle. In Mononchida and Dorylaimida, the rectal glands in the male consist of three to five pairs of cells located dorsolaterally or laterally from the posterior intestine (prerectum), caudally or dorsocaudally from the spicules their ducts form loops, run anteriorly between the spicules, and open into the dorsal wall of the cloaca. The S-E system (secretory-excretory) has been a key feature in differentiating the free-living aquatic nematode taxa with a glandular system with a well-developed ventral gland or renette cell.

Reproduction in many nematodes is sexual, involving males and females (=gonochorism; Gk. *gonos* = offspring, *chorismos* = separation) and occurs by amphimixis (Gk. *amphi* = both; *mixis* = mingling) or cross-fertilizing. Uniparental reproduction or autotoky has arisen independently in different taxa throughout the phylum. It can occur through automixis (Gk. *auto* = self) or self-fertilization in bisexual individuals that are protandrous hermaphrodites with one set of gametes (male) maturing before the other; cross-fertilizing hermaphrodites are unknown. Another method of autotoky takes the form of parthenogenesis (Gk. *parthenos* = virgin; *genesis* = descent) where development proceeds without fertilization. Asexual reproduction or parthenogenesis is common in plant parasitic nematodes. The male reproductive system basically has two testes (diorchic) that open in a common duct, the vas deferens; the posterior testis is usually reflexed. In monorchic males, a single testis is present upon reduction of the posterior (usually) or anterior testis. Spermatogenesis takes place in the testis but spermatids are usually activated into mature sperm after mating in female (hermaphrodite) uterus. The copulatory apparatus consists of two cuticularized spicules, rarely fused (*Rhabditis*) or reduced to a single spiculum or absent, and the associated gubernaculum. It functions by means of spicule and gubernaculum protractor and retractor muscles (Fig. 9.6 G). In Triplonchida, the spicule protractor muscles form a capsule of suspensor muscles that are not directly attached to the spicules. The gubernaculum may be complex or simple; in Dorylaimida only the lateral guiding pieces (crura) remain (Fig. 9.6 D). In the cloacal region and caudal region, accessory genital structures such as genital papillae or setae or cuticular extensions (bursa) may be present (Fig. 9.5 I). Basically, the female reproductive system has two uteri (**didelphic**), opposed (**amphidelphic**) and connected to a single vagina. Each genital branch consists of a gonad (ovary) and a gonoduct (oviduct and uterus) (Fig. 9.6 A). Reduction of one of the genital branches to a different degree is not uncommon: complete loss of a branch is indicated as the monodelphic condition (Fig. 9.6 B), whereas reduction of one ovary to various degrees of reduction of the gonoduct is indicated as **pseudomonodelphic**. When the vulva is displaced posteriorly on the body, the two (one) uteri are anteriorly directed (prodelphic condition), the opposite is indicated as opisthodelphic. The vulva may show different types of differentiations/appendages. In the family Oncholaimidae a tubular system, known as the **demanian** system, connects the reproductive system by a duct to a specialized part of the intestinal wall, the **osmosium**.

MATERIAL PREPARATION AND PRESERVATION

Immediate fixation in the field is typically recommended and widely in use for both quantitative community analysis and taxonomic purposes. Care must be taken (see Hodda & Abebe, 2006) as nematodes may adhere to the substrate. Therefore, several authors (e.g., Palmer et al., 2006; Giere, 2009; Hodda & Abebe, 2006) discuss relaxant approaches to overcome this effect. These include heat (not to be used for molecular analyses material) and distilled water, which should not only detach the specimens from the substrate but also cause them to stretch their bodies which will facilitate identification. Fixation without prior relaxation is often warned against because of obtaining mostly coiled animals. However, observations on freshwater nematodes over a range of various studies have shown extremely low numbers of coiled individuals, and those mainly of *Tripyla* and some tobrilid genera. The vast majority of individuals were uncoiled, slightly bent, but well-preserved specimens

from immediate fixation (mostly with 4%−10% formalin, less often with DESS). Nevertheless, a comprehensive evaluation of different methodological approaches with potential advantages and disadvantages is needed.

The simplest method to use is a low formalin concentration (4%−10%) for fixation and preservation. Other formaldehyde-containing mixtures may be used (e.g., FA, FAA, TAF, FP, but see formulae at end of this section). Since formalin poses health concerns, its use may increase administrative and logistic sample pre-preparation as well as complicate shipping. DESS represents an alternative consisting of EDTA, NaOH, and $DMSO_4$. Though preparation takes some time, it provides properly fixed nematodes for microscopic analyses (light and electron) (Yoder et al., 2006). The additional advantage of DESS is its use for specimens for molecular analyses. Morphological and molecular analyses can be done with the same sample material using DESS, which is not possible with formalin or alcoholic material. The former impedes PCR, while the latter causes specimen deformation. DESS-fixed and glycerol-dehydrated nematode specimens should not be stored on slides for more than 2 weeks prior to molecular analysis (Bik et al., 2009).

When using DESS, most of the water that comes with the specimens must be eliminated, ideally by sieving (38−40 µm) or replacing the DESS solution after several hours. Minimum preservation times prior to further processing range from 2 to 14 days, at least for formalin-preserved material. Subsequent processes include elutriation, decantation, or centrifugation (but see Hodda & Abebe, 2006). Centrifugation with Ludox® has become a standard to facilitate sorting. Procedures are given by Hodda and Abebe (2006), Palmer et al. (2006), and Vincx (1996). Fixed samples should be washed prior to Ludox® centrifugation. Centrifuge tubes (50, 250, 500 mL; large tubes are better than small tubes) are filled with sediment and a solution of Ludox® TM50 (adjusted density: 1.14 g/cm^3). The sediment should not exceed 1/8 to 1/5 of tube volume. After gently mixing, tubes are centrifuged at 1600−1800 g for 3−5 min; up to three runs will sufficiently gather most of the nematode material. Hodda and Abbebe (2006) and Palmer et al. (2006) recommend low-speed centrifugation at 300 g and 500−1550 rpm, respectively. Prior testing and method standardizing for a given habitat/substrate is advantageous for quantitative analyses. Staining with Rose Bengal (1 g in 10% formalin solution) increases nematode visibility and generally facilitates sorting, regardless of substrate type.

Subsample preparation helps decrease sorting time when quantitative data are needed. Once sorted, fixed nematodes must be dehydrated before being mounted on permanent slides in glycerin. A slow procedure (Seinhorst, 1959) generates well-prepared nematodes for light microscopic studies. Nematodes are placed in small glass containers (e.g., Bovery dish) about half-filled with solution I [79% distilled water, 20% ethanol (96%), 1% glycerol], left covered (in a Petri dish or desiccator) at room temperature (at least 24 h) or in an incubator (35−40°C, 16 h). Then the first solution can be carefully removed, or containers are carefully restocked with solution II (95% ethanol 96%, 5 ml glycerol; alternative 93:7), covered and stored at room temperature or in an incubator (35−40°C) for 48 h or 2−3 days, respectively (or until the alcohol is evaporated and seemingly only pure glycerol is left). We recommend covering the containers at least partially to prevent collecting dust. After one to two droplets of water-free glycerol have been added to the (cooled) containers, storage in a desiccator with $CaCl_2$ for at least 2 more days, guarantees the nematodes are in pure glycerol. Fine needles (also insect needles with a hook-like curved tip), fine pipettes, wire loops, and eyelashes fixed on a handle can be used for transfer steps.

Readily dehydrated nematodes are transferred from pure glycerol storage into a drop of glycerine on a slide; 5−10 nematodes are an appropriate number per slide. It is advantageous to put similarly sized nematodes together on one slide. Glass or wire fibers can be placed at the edges of the glycerol drop (or into its borders) to prevent nematodes from being squashed. Finally, a coverslip is let down very carefully and sealed with nail polish or an alternative sealing application. An alternative approach is sealing with paraffin: a paraffin ring is placed on a slide, within it are placed glycerol and nematodes. This is covered by a coverslip and then slightly heated, which melts the paraffin and seals the coverslip. In general, it is important to use not too much or too little glycerol and to make sure the nematodes do not overlap and are arranged in the middle and the bottom of the glycerol droplet.

FA 4:1
10.8 mL 37% formaldehyde
1 mL glacial acetic acid

FAA
50 mL 95% ethanol
35 mL distilled water
10 mL 37% formaldehyde solution
5 mL glacial acetic acid

FP 4:1
10.8 mL 37% formaldehyde
1 mL propanoic acid
88.2 mL distilled water

KEYS TO NEMATODA

In recent decades, classifications have been the result of a more holistic approach by combining morphology with molecular data. Higher-level taxa, such as subclass, order, or suborder, appear less clearly defined by morphological characters since some characters are not always expressed; and if they are, synapomorphies are not always distinct characters suitable for identification. For example, Triplonchida are characterized by the synapomorphy in males where the protractor muscles are not directly attached to the spicules but form a capsule of suspensor muscles, a feature not always clearly visible in some families and showing a progressive evolution. Another example of synapomorphy, is the presence of metanemes in Enoplida. Furthermore, for several taxa, molecular data are limited and consequently relationships are still unclear. We have tried to accommodate as much as possible, the option for separate keys at order, family and genus level where possible. We follow the general classification of De Ley and Blaxter (2004) as far as possible, completed by identification keys from the most recent books on freshwater nematodes (Abebe et al., 2006), the Handbook of Zoology (Schmidt-Rhaesa, 2014), and the recent books on free-living nematodes of Hungary I, II, and III by Andrássy (2005, 2007, 2009).

Nematoda: Orders

Genera that are not typically freshwater, but are associated with submerged aquatic plants or semiaquatic habitats/soils are designated with an asterisk (*).

1	Body without desmen; amphidial fovea not vesicular; 4 cephalic setae (cs) not on peduncles 2
1′	Body cuticle annulated and covered by rings of foreign particles (desmen); amphidial fovea vesicular, four cs inserted on peduncles (Fig. 9.3 A) ..... Desmoscolecida: one genus *Desmoscolex**
2(1)	Body distinctly shorter than 1 cm; pharynx not a stichosome (= pharynx disconnected from intestine by pharyngeal gland cells) 3
2′	Body filiform, usually >1 cm long; mouth closed; pharynx a stichosome; juveniles parasites in invertebrates (Fig. 9.3 D) ..... Mermithida, one family: Mermithidae
3	Buccal cavity with a protrusible stomatostylet (Fig. 9.2 B); pharynx with valved metacorpus 4
3′	Buccal cavity with different type of stylet (odontostyle, onchiostyle) or with teeth or unarmed 5
4	Stomatostylet very fine; dorsal pharyngeal gland orifice in metacorpus ..... **Aphelenchida**
4′	Stomatostylet stronger; dorsal pharyngeal gland orifice in procorpus, usually shortly posterior to base of stylet knobs ..... **Tylenchida**
5(3)	Pharynx variable (unipartite or subdivided); stoma either unarmed or with teeth (tooth); no double adanal supplement in male 6
5′	Pharynx posteriorly widened to a more or less fusiform expansion (Fig. 9.5 D); stoma with protrusible odontostyle or a single ventrosublateral mural tooth (Fig. 9.4 O) or odontostyle surrounded by four onchia (teeth) (Fig. 9.2 C), with or without denticles; adanal precloacal supplements in male double (Fig. 9.6 D) ..... **Dorylaimida**
6(5)	Stoma either unarmed or with teeth (tooth); pharynx variable 7
6′	Stoma with a complex protrusible tooth or onchiostyle (Fig. 9.2 D); pharynx with posterior enlargement ..... Triplonchida: **Diphtherophorina**
7(6)	Pharynx cylindrical (can be widened posteriorly) (Fig. 9.5 B) (e.g., Enoplida: Alaimina, Andrassyidae, Oxystomatidae) 8
7′	Pharynx subdivided, posteriorly expanded (bulb-like) or with median and basal expansion 12
8(7)	Cardia without large glandular cells 9
8′	Cardia with large, distinctly round, ovoid, or elongated glandular cells (mostly three, seldom more), cephalic sensilla setiform [sometimes setiform papilla (1.5−2 µm), papilliform (≤1 µm) in *Tobrilia*], buccal cavity variable, narrow with three small denticles (Tripylidae), spacious with small denticles or large teeth; amphidial fovea pocket-shaped [sometimes hard to see in light microscopy (LM)] or dorsally spiral ..... **Triplonchida**
9(8)	Amphidial fovea with rounded outline (circular or spiral); stoma small to medium-sized, with or without small teeth (denticles) 10
9′	Amphidial fovea without rounded outline; stoma variable, unarmed or armed 11
10(9)	Amphidial fovea unispiral or derived therefrom; S-E system opening in cheilostom; female reproductive system didelphic with reflexed ovaries ..... **Plectida: Aphanolaimidae**
10′	Amphidial fovea circular (Fig. 9.3 K); S-E system opens at level pharynx; female reproductive system predominantly monodelphic (exc. two ovaries in *Terschellingia*), with outstretched ovary (ovaries) (exc. reflexed in *Sinanema*) ..... **Monhysterida**
11(9)	Stoma large, strongly sclerotized with large tooth/teeth (Fig. 9.4 A), with or without denticles/ventrosublateral ridges (exc. cylindrical Cryptonchidae); anterior sensilla papilliform, arranged in two circlets on lip region; amphidial fovea small cup-shaped and aperture slit-like (Fig. 9.3 N); no somatic setae; caudal glands present or absent, never extending precaudally ..... **Mononchida**
11′	Stoma variable (large, narrow cylindrical or very small), with or without armature (tooth/teeth or mandibles); anterior sensilla papilliform and setiform arranged in two or three circlets; amphidial fovea and aperture variable; somatic setae can be present; caudal glands absent or present, can extend precaudally ..... **Enoplida**
12(7)	Pharynx only posteriorly widened, with or without marked end bulb 13
12′	Pharynx tripartite (with an anterior and posterior expanded part (Fig. 9 4 D) 16
13(12)	Pharynx posteriorly enlarged, if bulb present, then neither with a complex valvular apparatus or an elongated muscular cardia 14

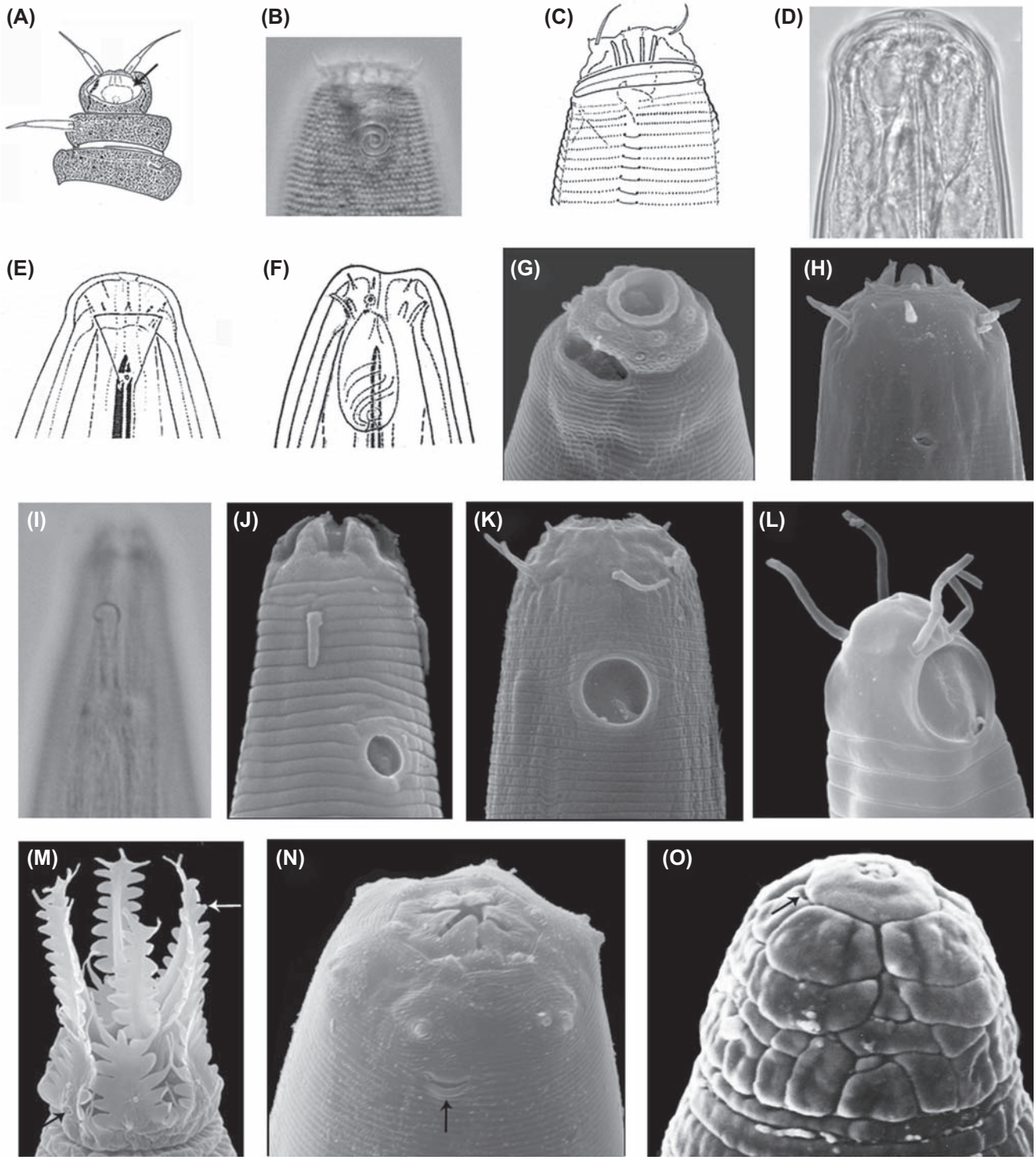


FIGURE 9.3 Head region with amphid: (A) vesicular fovea in *Desmoscolex*; (B) multispiral fovea in; (C) flattened unispiral fovea (*Ptycholaimellus*); (D) nonfeeding male of a mermithid; (E) infundibuliform fovea with incisiform opening in *Xiphinema*; (F) pouch-like fovea and pore-like opening in *Longidorus*; (G) oblique front view of a dorylaimid showing the wide amphidial opening leading to an inner poculiform fovea; (H) small incisiform opening in a tobrilid; (I and J) rounded fovea in a plectid (LM and SEM); (K) circular fovea in a monhysterid; (L) rounded fovea in an aphanolaimid; (M) pore-like amphid opening (*black arrow*), white arrow points to a tine of labial probolae in *Acrobeles*; (N) incisiform amphid opening of a small inner pocket-like fovea in a mononchid; and (O) incisiform amphid opening at border oral disc in *Scutellonema*. *(C) From Decraemer & Coomans (1978), courtesy of the Australian Journal of Marine and Freshwater Research; (D) Gradinarov (2014), courtesy of Zookeys; and (M) courtesy of J. Baldwin.*

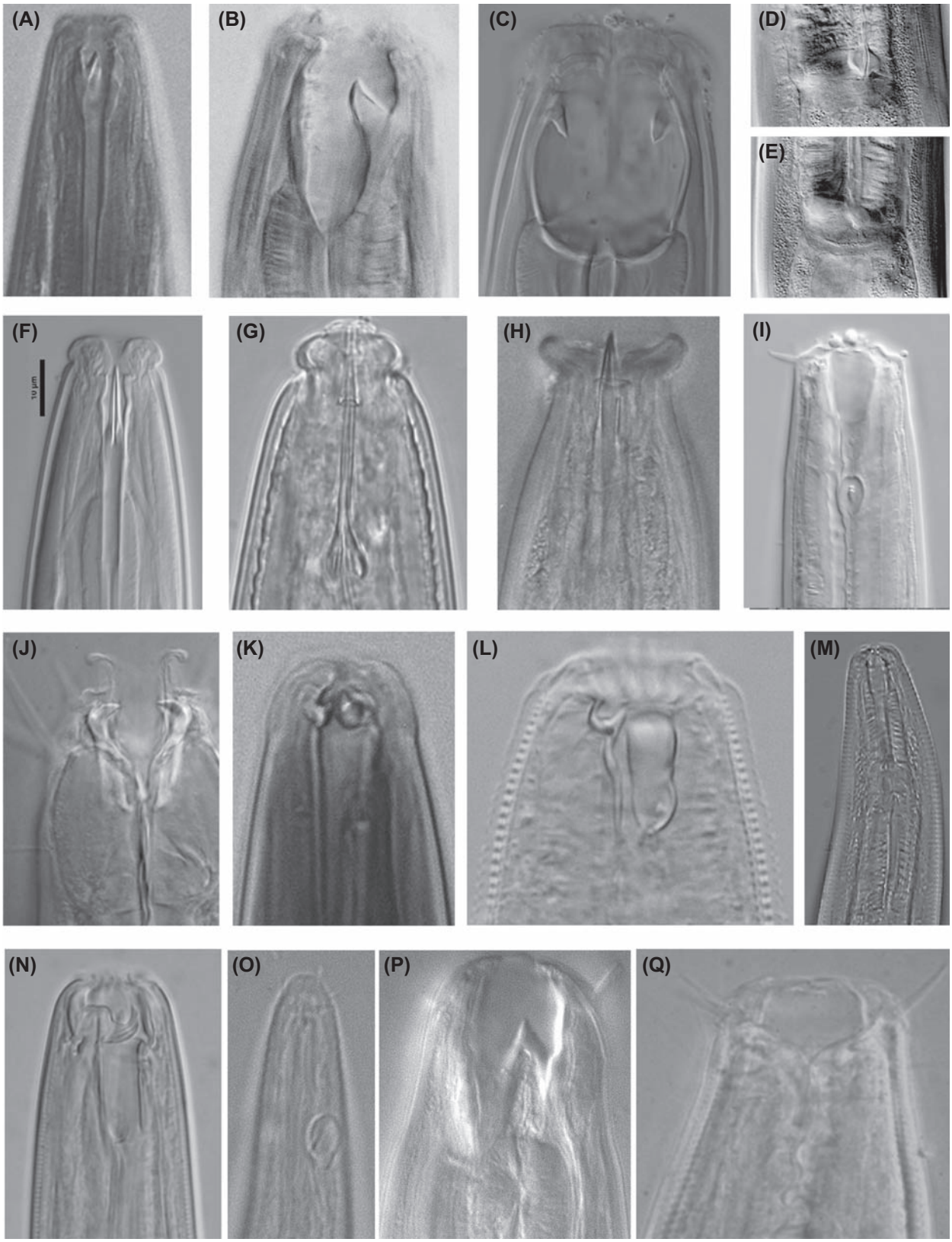


FIGURE 9.4 Different types of stoma and armature: (A) stoma with ventrosublateral tooth in *Oionchus* (Mononchida); (B) large dorsal tooth *Mylonchus* (Dorylaimida); (C) retrorse teeth in *Anatonchus* (Mononchida); (D and E) tuberculate cardia in Anatonchidae; (F) axial ventrosublateral stylet in *Nygolaimus*; (G) odontostyle with basally flanged odontophore in *Tylencholaimus*; (H) discolaimus; (I) posterior stomatal pocket with teeth in focus in *Neotobrilus*; (J) mandibles in *Enoploides*; (K) long stoma with three equal movable teeth anteriorly in *Ironus*; (L) large dorsal tooth and small ventrosublateral teeth (not in focus) in *Achromadora*; (M) cylindrical gymnostom in *Plectus*; (N) movable teeth in *Mononchoides*; (O) *Leptolaimus* with focus on rounded fovea; (P) large right ventrosublateral tooth in *Oncholaimus*; and (Q) wide stoma without teeth in *Theristus*. *(F) Courtesy of R. Pena-Santiago; (G and I) from Abebe et al. (2013), courtesy of the Journal of Nematology; and (N) from Steel et al. (2000), courtesy of the Journal of Nematology.*

13′	Pharynx either with a basal bulb with complex valvular apparatus or an extremely elongated muscular cardia (Fig. 9.5 A)	**Plectida (exc. Aphanolaimidae)**
14(13)	Body cuticle not punctated, strongly annulated or finely striated or smooth	15
14′	Body cuticle punctated (Fig. 9.3 A)	**Chromadorida**
15(14)	Stoma cylindrical, armed or unarmed; cheilostom without 12 rhabdia	**Araeolaimida**
15′	Cheilostom with 12 weak cheilorhabdia, pharyngostom more or less conical, with small teeth (one dorsal and two ventrosublateral); pharynx with posterior rounded bulb	**Desmodorida**
16(12)	Pharynx with two only slight swellings, one median and one posterior, the latter encircled by cells, no valvae, tail with caudal glands	Plectida: Ohridiidae: one genus: *Domorganus*
16′	Pharynx with at least one distinct valvate bulb either median or posterior, tail without caudal glands	**Rhabdidita**

Nematoda: Aphelenchida: Families and Genera

1	Pharynx with overlapping dorsal gland, without offset basal bulb	2
1′	Pharynx with pyriform basal bulb, offset from intestine	Paraphelenchidae: one genus: *Paraphelenchus**
2(1)	Male without well-developed bursa	3
2′	Male with well-developed bursa with genital papillae (rays)	Aphelenchidae: one genus: *Aphelenchus**
3(2)	Tail elongate filiform in both sexes	Seinuridae, one genus: *Seinura**
3′	Tail short in both sexes	Aphelenchoididae, one genus: *Aphelenchoides*

Nematoda: Tylenchida *Sensu* Siddiqi (2000) and Andrássy (2005): Families

1	Cuticle either finely striated or coarsely annulated with annulae retrorse and often provided with cuticular outgrowths (scales, spines); pharynx criconematoid = with large median bulb amalgamated with procorpus and isthmus either slender or short and amalgamated with basal bulb (Fig. 9.5 F)	2
1′	Cuticle finely or coarsely annulated or smooth, provided with lateral fields; pharynx with procorpus offset from median bulb, glandular region of bulb either bulbous offset or lobiform overlapping intestine	6
2(1)	Cuticle thick, coarsely annulated and often with outgrowths, isthmus broad and fused with basal bulb	3
2′	Cuticle thin, finely annulated without outgrowths; isthmus slender, basal bulb separated	5
3(2)	Cuticular annulae rounded, without appendages; male tail long, bursa high	4
3′	Cuticular annulation retrorse, often with appendages; male tail short, bursa if present low	**Criconematidae**
4(3)	Females and juveniles with a sheath-like second cuticle	Hemicycliophoridae: one genus *Hemicycliophora*
4′	Sheath-like cuticle membranous, very thin and often hardly discernible	Caloosiidae, one genus: *Caloosia**
5(2)	Adult female elongate obese; pharyngeal procorpus slender, stylet short	**Tylenchulidae**
5′	Female vermiform broad; isthmus and basal bulb separated; rounded stylet knobs	Paratylenchidae, one genus: *Paratylenchus*
6(1)	Mature female strongly swollen, sessile	7
6′	Mature female vermiform	9
7(6)	Mature female spherical, lemon, pear-shaped; male with well-developed stylet and pharynx	8
7′	Mature female saccate or fusiform; male degenerate or lacking stylet/pharynx; S-E pore posterior to median bulb	Rotylenchulidae: one genus: *Rotylenchulus*
8(7)	S-E pore posterior to median bulb	Heteroderidae, one genus: *Heterodera*
8′	S-E pore anterior to median bulb	Meloidogynidae, one genus: *Meloidogyne**
9(6)	Head without setae	10
9′	Head with four long setae (rare, semiaquatic)	Atylenchidae: one genus*: Atylenchus*
10(9)	Female reproductive system prodelphic	11
10′	Female reproductive system amphidelphic	14
11(10)	Body not extremely attenuated to stout; bursa not lobed	12
11′	Body extremely attenuated; bursa often lobed	**Ephyadophoridae**

12(11)	Bursa not enveloping tail terminus	13
12′	Bursa enveloping tail terminus	**Pratylenchidae** (in part)
13(12)	Bursa short adanal; sperm cells small	**Tylenchidae**
13′	Bursa subterminal reaching beyond midtail; sperm cells large	Anguinidae: one genus: *Ditylenchus*
14(10)	Pharyngeal glands lobed	15
14′	Pharyngeal glands in bulb or only dorsal gland extending over intestine	16
15(14)	Cephalic region low, bursa with phasmidial pseudoribs	**Pratylenchidae** (in part)
15′	Cephalic region elevated, high-arched; bursa without phasmidial pseudoribs	**Hoplolaimidae**
16(15)	Tails dissimilar between sexes, not filiform; bursa enveloping entire tail	17
16′	Tails similar in both sexes, mostly filiform; bursa adanal	Psilenchidae, one genus: *Psilenchus**
17(16)	Cephalic region generally quadrilobate, cone much longer than rest stylet	18
17′	Cephalic region rounded, cone about 50% of stylet length	**Telotylenchidae**
18(17)	Pharyngeal glands located in basal bulb; bursa trilobed	Dolichodoridae: one genus *Neodolichodorus**
18′	Dorsal pharyngeal gland overlapping intestine; bursa simple	Belonolaimidae: one genus *Belonolaimus**

Nematoda: Tylenchida: Criconematina: Criconematidae: Genera

1	Female without cuticular sheath	2
1′	Female body with cuticular sheath giving appearance of double cuticle (Fig. 9.5 F)	*Hemicriconemoides**
2(1)	Annulae in females without scales or spines; juveniles either with or without scale/spines	3
2′	Annulae in both female and juvenile ornamented with scales or spines	*Ogma*
3(2)	Both juvenile and female annulated cuticle smooth, without scales or spines	*Criconemoides*
3′	Only juvenile cuticle with longitudinal rows of scales; head with two annulae, submedian lobes when present, poorly developed	*Criconema*

Nematoda: Tylenchida: Tylenchulidae: Genera

1	Female elongate-obese, slightly curved ventrally; secretory-excretory pore at 70%−80% of body length	*Tylenchulus**
1′	Female saccate, very strongly curved ventrally; secretory-excretory pore at midbody	*Trophotylenchulus**

Nematoda: Tylenchida: Ephyadophoridae: Genera

1	Body abruptly narrowing posterior to vulva; bursa well developed, lobiform	*Ecphyadophora*
1′	Body very slender not narrowing posterior to vulva; bursa less developed, not lobiform	*Lelenchus**

Nematoda: Tylenchida: Tylenchidae: Genera

1	Cuticle provided with longitudinal ridges, tessellate (block-like appearance)	2
1′	Cuticle without longitudinal ridges	3
2(1)	Vulva with lateral vulval membranes	*Coslenchus*
2′	Vulva with ventral vulval membrane	*Pleurotylenchus*
3(2)	Amphidial aperture a conspicuous transverse slit at base of lip area	4
3′	Amphidial aperture pore-like and labial, or longitudinal slit-like (often oblique) postlabial	6
4(3)	Stylet with distinct basal knobs	5
4′	Stylet without basal knobs, conus asymmetrical	*Neopsilenchus*
5(4)	Body strongly ventrally curved to spiral; stylet knobs flanged	*Boleodorus**

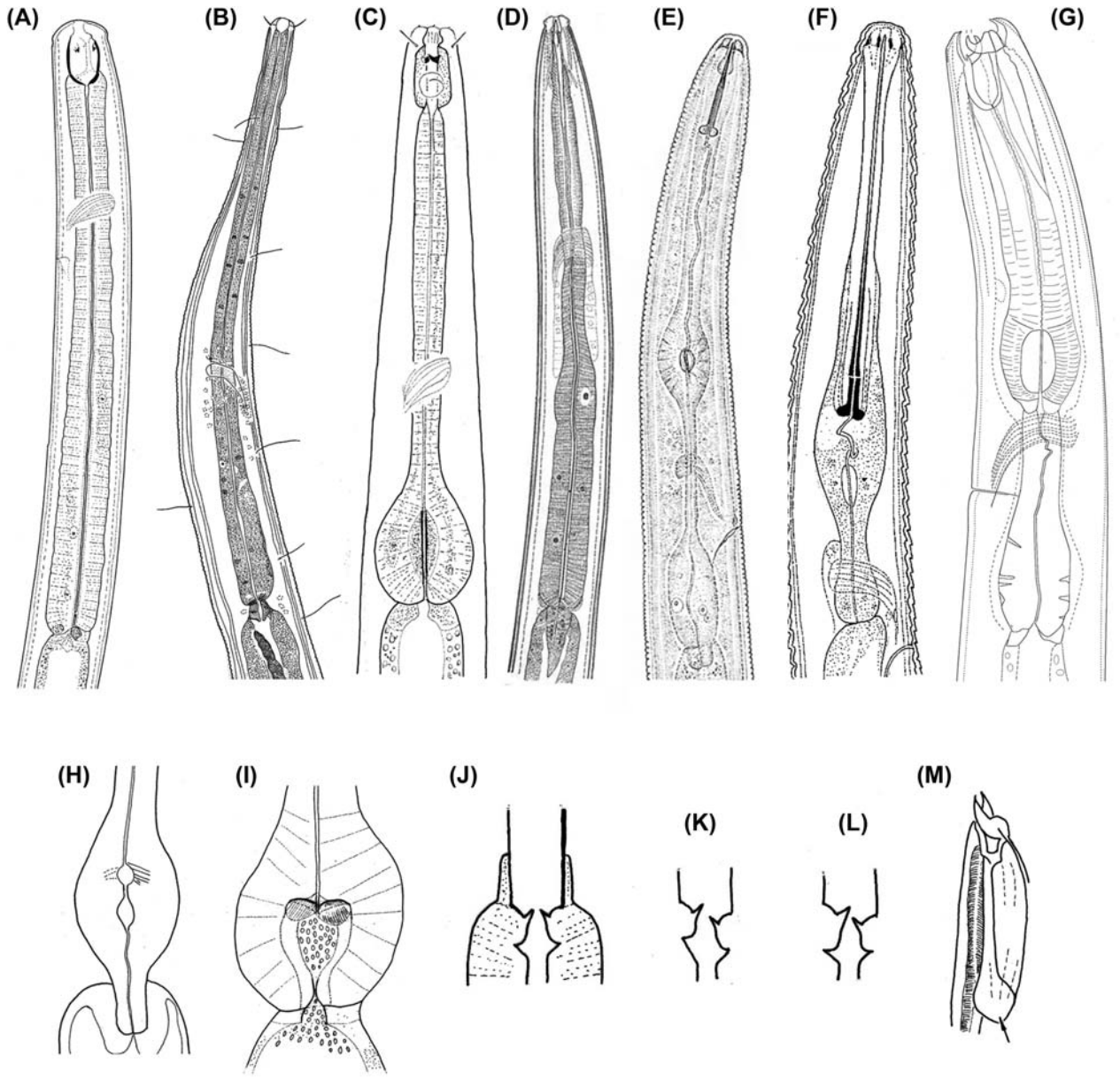


FIGURE 9.5 (A) Cylindrical pharynx (*Anatonchus*); (B) largely cylindrical slightly enlarged posteriorly (*Theristus*); (C) pharynx with anterior enlargement and posterior bulb (Ethmolaimus); (D) dorylaimid flask-shaped pharynx (*Labronema*); (E) tripartite pharynx with median and posterior bulb showing outlet of S-E system (*Amplimerlinius*); (F) tripartite pharynx with enlarged corpus and short isthmus typical for criconematids (*Hemicriconemoides*); (G) diplogasterid type of pharynx (*Mononchoides*); (H) a plectid valved pharyngeal bulb; (I) a rhabditid valved pharyngeal bulb; (J) an isomorphic, isotopic glottoid in metastegostom; (K) an isomorphic, anisotopic glottoid apparatus; (L) an anisomorphic glottoid apparatus; and (M) feeding apparatus in *Tylopharynx* pointing to apodeme. *(A) From Decraemer & Coomans (1978) courtesy of the Australian Journal of Marine and Freshwater Research; (D) from Ciobanu, Popovici & Decraemer (2004), courtesy of the Russian Journal of Nematology; (E) from Siddiqi (1976), courtesy of Nematologica; (F) from Decraemer & Geraert (1992), courtesy of Nematologica; and (G) from Steel et al. (2000), courtesy of Nematology; (J and K) redrawn from De Ley et al. (1998) in the Nematode Workshop Manual); and (M) redrawn from von Lieven & Sudhaus (2000), courtesy of the Journal of Zoological Systematic and Evolutionary Research.*

5′	Body straight or slightly curved; stylet slender, stylet knobs small round	*Basiria**
6(3)	Body annulation very prominent, deeply incised	7
6′	Body annulation normal, not deeply incised	8
7(6)	Body annulae with fine zigzag borders; male without bursa	*Miculenchus**

7′	Body annulae without zigzag borders; male with bursa	*Malenchus*
8(6)	Labial region continuous or slightly marked, not expanded; stylet at most two labial diameter	9
8′	Labial region expanded, well offset; stylet at least two labial diameters long	*Cephalenchus**
9(8)	Posterior uterine sac present; vulval membranes absent	10
9′	Posterior uterine sac absent; vulval membranes present	*Aglenchus*
10(9)	Stylet cone conspicuously shorter than shaft and knobs together; tail straight or slightly bent ventrally	*Filenchus*
10′	Stylet cone 50% of stylet length; tail always ventrally curved	*Tylenchus*

Nematoda: Tylenchida: Pratylenchidae: Genera

1	Female reproductive system amphidelphic	2
1′	Female reproductive system prodelphic	*Pratylenchus**
2(1)	Pharyngeal glands overlapping intestine mostly ventrally	3
2′	Pharyngeal glands overlapping intestine mostly dorsally	*Radopholus**
3(2)	Tail shape similar in both sexes; phasmid in posterior third of tail; tail end often mucronate	*Hirschmanniella*
3′	Tail shape dissimilar between sexes; phasmid at midtail; tail end not mucronate	*Zygotylenchus**

Nematoda: Tylenchida: Hoplolaimidae: Genera

1	Phasmids large, scutellum-like, mostly not opposite each other on lateral sides	2
1′	Phasmids small, opposing one another or lacking	4
2(1)	Stylet knobs rounded	3
2′	Stylet knobs tulip-like with anterior projections	*Hoplolaimus**
3(2)	Scutella in or near anal region, close to each other (Figs. 9.3 O and 9.6 H)	*Scutellonema**
3′	Scutella far anterior to anus, separated from each other	*Peltamigratus**
4(1)	Pharyngeal glands overlapping intestine ventrally or ventrolaterally	*Helicotylenchus*
4′	Pharyngeal glands overlapping intestine dorsally or dorsolaterally	*Rotylenchus**

Nematoda: Tylenchida: Telotylenchidae: Genera

1	Lateral field with six incisures	2
1′	Lateral field with 3–5 incisures	4
2(1)	Female tail conoid or subcylindrical; end cuticle at most slightly thickened	3
2′	Female tail cylindrical, with abnormally thickened cuticle at distal end	*Amplimerlinius*
3(2)	Labial annulae simple, not interrupted by grooves	*Nagelus*
3′	Labial annulae interrupted by radial grooves	*Geocenamus**
4(1)	Labial annulae with lateral indentations; outer bands of lateral field areolated (Fig. 9.6 H)	*Bitylenchus**
4′	Labial annulae without lateral indentations; outer bands generally not areolated	*Tylenchorhynchus*

Nematoda: Dorylaimida: Families

1	Feeding apparatus as a mural tooth inserted on one of the ventrosublateral sectors of the pharynx (Fig. 9.4 F); tail shape similar in male and female	Nygolaimina 2
1′	Feeding apparatus as an axial odontostyle inserted on an odontophore with or without knobs or flanges; tail shape in male and female similar or different	Dorylaimina 3

2(1)	Female reproductive system mono-opisthodelphic; male unknown; pharyngeal expansion surrounded by a distinct spiral sheath; three small ovoid cardiac cells ..... Nygellidae, one genus: *Nygellus*
2′	Female reproductive system didelphic; males present; pharyngeal expansion long (about 50% of pharynx length), sometimes surrounded by a weak sheath; three large cardiac cells ..... **Nygolaimidae**
3(1)	Enlarged pharyngeal part not surrounded by muscular sheath 4
3′	Enlarged pharyngeal part always surrounded by a well-discernible muscular sheath ..... **Belondiridae**
4(3)	Pharyngeal posterior bulbiform expansion reduced to a cylinder or pyriform bulb, shorter than a third of total pharynx 5
4′	Pharyngeal posterior expansion longer than a third of total pharynx, not short and bulbiform 8
5(4)	Pharynx bipartite 6
5′	Pharynx tripartite: long slender anterior part gradually widening posteriorly to a narrow glandular midportion and a pyriform basal bulb with pronounced valvar chamber ..... Aulolaimoididae, one genus: *Aulolaimoides*
6(5)	Cuticle not tylencholaimoid 7
6′	Cuticle tylencholaimoid with inner layer separated from outer layer and provided with radial refractive elements .... **Tylencholaimidae**
7(6)	Odontostyle asymmetrical with shorter ventral arm, wide opening; pharyngeal bulb 1/4th to 1/3rd of total pharynx ..... **Mydonomidae**
7′	Odontostyle symmetrical, tubular, usually with small opening; pharyngeal bulb pyriform, 1/4th to 1/5th of total pharynx ..... **Tylencholaimellidae**
8(4)	Cheilostom usually narrower, never armed with four onchia around odontostyle 9
8′	Cheilostom wide, usually well-sclerotized, armed with four onchia surrounding the odontostyle ..... **Actinolaimidae**
9(8)	Odontostyle not long and thin; if thin then short 10
9′	Odontostyle extremely long and thin with fine lumen and aperture, body long ..... **Longidoridae**
10(9)	Odontostyle aperture shorter than half its length 11
10′	Odontostyle aperture longer than half of its length ..... **Aporcelaimidae**
11(10)	Lip region prominent, two circles of labial papillae far apart; gubernaculum present or absent; vagina with or without sclerotized pieces 12
11′	Lip region low, not offset, two circles of labial papillae close to each other; gubernaculum present; vagina swollen, without sclerotized pieces ..... **Thorniidae**
12(11)	Odontostyle not very long, with wide lumen and aperture 13
12′	Odontostyle slender, more or less long, with narrow lumen and aperture ..... **Nordiidae**
13(12)	Female tail elongate to filiform; male tail generally short, rarely as in female; lateral guiding piece (Fig. 9.6 D) usually present ..... **Dorylaimidae**
13′	Tail similar in both sexes, short conoid to rounded; no gubernaculum ..... **Qudsianematidae**

Nematoda: Dorylaimida: Nygolaimidae: Genera

1	Cardiac glands ovoid to spherical; pharyngeal gland nuclei not enlarged; vulva transverse, no paravulvae present 2
1′	Cardiac glands longer than wide; pharyngeal gland nuclei unusually large; vulva longitudinal, advulvar region ventrally with some large papilla or pore-like organs (paravulvae) ..... *Paravulvus*
2(1)	Mural tooth deltoid, linear or dorylaimoid with lumen; lip region continuous or offset 3
2′	Mural tooth aciculate, without lumen; lip region mostly set off by constriction ..... *Solididens*
3(2)	Mural tooth deltoid or linear, without apparent aperture and narrow lumen 4
3′	Mural tooth dorylaimoid, with a distinct lumen and anterior oblique wall resembling the dorsal aperture of an odontostyle ..... *Laevides*
4(3)	Lip region continuous with adjacent body or slightly marked by depression; tooth linear or deltoid 5
4′	Lip region offset by a constriction; mural tooth deltoid; male ventromedian precloacal supplements weak or lacking, gubernaculum absent (Fig. 9.4 F) ..... *Nygolaimus*
5(4)	Body about straight upon fixation; mural tooth linear, tail convex–conoid or hemispherical, never clavate ..... *Aquatides*
5′	Body ventrally curved upon fixation; mural tooth deltoid to linear; tail hemispherical to clavate ..... *Clavicaudoides*

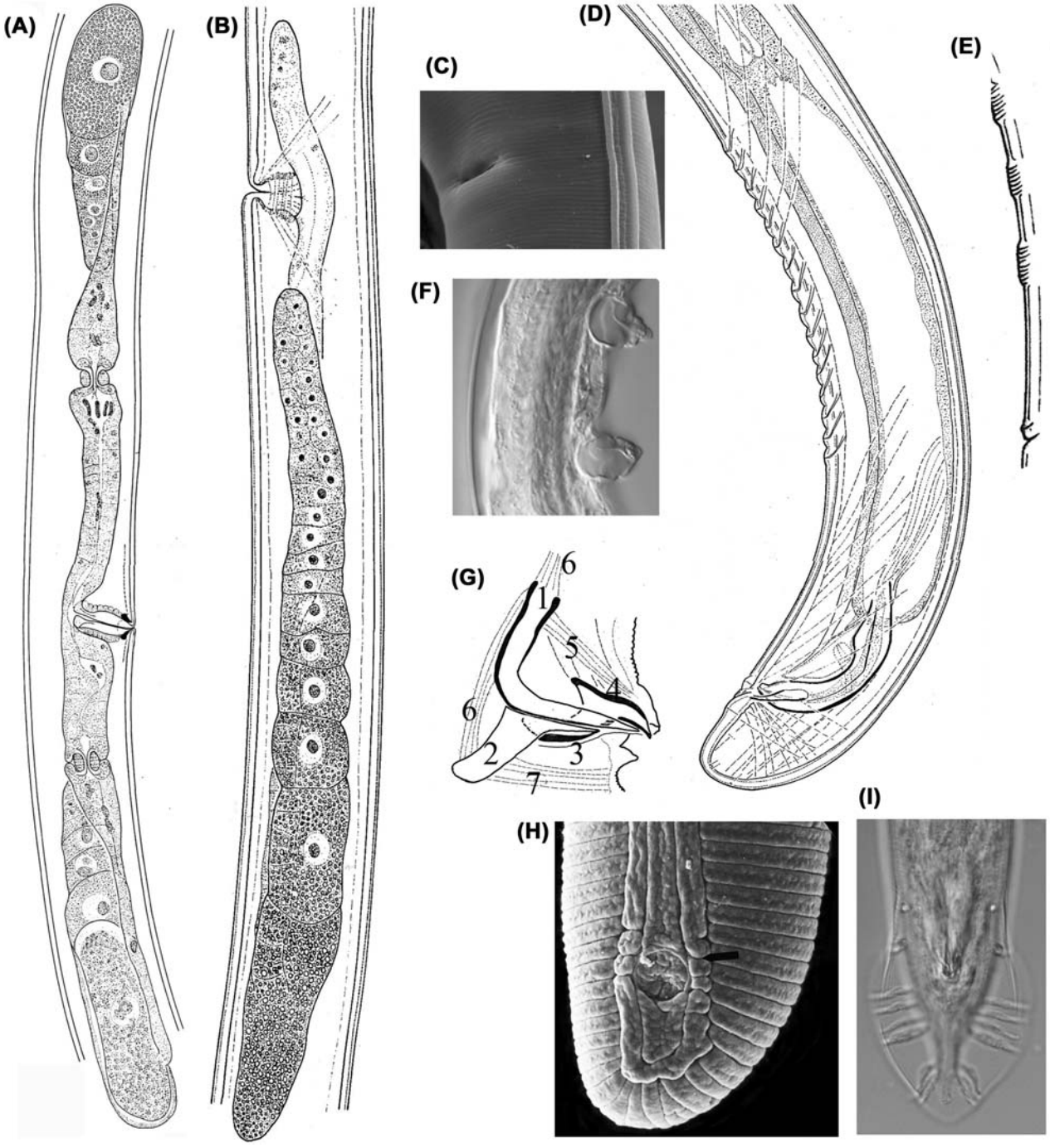


FIGURE 9.6 (A) Female didelphic amphidelphic reproductive system (*Mesodorylaimus*); (B) monodelphic opisthodelphic female reproductive system (*Doryllium*), (C) vulva region in plectids, showing also ridges in lateral field; (D) posterior body region in a dorylaimid male showing pair of precloacal supplements at some distance from series of ventromedian supplements and dorylaimid spicule (*Labronema*); (E) precloacal supplements arranged in fascicles; (F) large precloacal supplements in a tobrilid (*Neotobrilus*); (G) copulatory apparatus (*Theristus*) and associated spicule protractor muscles (5), retractor muscles (6), and gubernaculum retractor muscles (7) and parts of gubernaculum: 2 = dorsal apophyse, 3 = corpus, 4 = cuneus; (H) female tail of *Scutellonema* showing lateral field with scutellum and alveolar ornamentation of ridges lateral field (*arrow*); and (I) ventral view of male tail with bursa and genital papillae (rays) in *Caenorhabditis*. *(A, B, and D) From Ciobanu, Popovici, & Decraemer (2004), courtesy of the Russian Journal of Nematology; (F) from Abebe et al. (2013), courtesy of the Journal of Nematology; (G) from Decraemer & Coomans (1978), courtesy of the Australian Journal of Marine and Freshwater Research; and (I) courtesy of Dieter Slos.*

Nematoda: Dorylaimida: Belondiridae: Genera

1	No sclerotized pieces around mouth; odontophore bacilliform, not flanged	2
1′	Four sclerotized pieces present around oral opening; odontophore flanged	*Dorylaimellus*
2(1)	Tail at least in female long filiform; odontostyle short, slender	3
2′	Tail in both sexes short rounded to conoid; odontostyle rather short but robust, odontophore bacilliform	*Axonchium*
3(2)	Tail filiform in both sexes; odontostyle slender with aperture occupying about half of total length; lip region continuous, rounded, or weakly angular in lateral view	*Oxydirus*
3′	Tail dissimilar in both sexes, long in female, short, rounded in male; odontostyle very thin, short, with small aperture; lip region continuous, rounded	*Lindseyus*

Nematoda: Dorylaimida: Tylencholaimidae: Genera

1	Odontophore with small basal knobs, lip region cap-like, offset by constriction or depression; males known (Fig. 9.4 G)	*Tylencholaimus*
1′	Odontophore without basal knobs; lip region cap-like, strongly offset by constriction; male unknown	*Meylonema*

Nematoda: Dorylaimida: Mydonomidae: Genera

1	Tail shape similar in both sexes, elongate conoid to filiform	2
1′	Tail shape different in male and female, elongate in female, short and rounded in male	*Morasia*
2(1)	Body long, usually more than 4 mm; odontophore straight, sclerotized	*Calolaimus*
2′	Body medium-sized, mostly 1−2 mm; odontophore arcuate or angular	*Dorylaimoides*

Nematoda: Dorylaimida: Tylencholaimellidae: Genera

1	Odontostyle short tubular lacking accessory pieces, odontophore with distinct basal knobs or flanges (Fig. 9.6 B)	*Doryllium*
1′	Odontostyle short tubular with dorsal accessory piece; odontophore with basal knobs	*Tylencholaimellus*

Nematoda: Dorylaimida: Actinolaimidae: Genera

1	Cheilostom not or only weakly sclerotized	2
1′	Cheilostom walls strongly ribbed, basket-like	*Westindicus*
2(1)	Cheilostom wall with denticles	3
2′	Cheilostom wall without denticles	4
3(2)	Male supplements in series	*Paractinolaimus*
3′	Male supplements in fascicules (Fig. 9.6 A)	*Afractinolaimus*
4(2)	Male supplements in series	5
4′	Male supplements in fascicules	*Neoactinolaimus*
5(4)	Pharynx bipartite	*Egtitus*
5′	Pharynx tripartite with a slender anterior part, a gradually expanded midpart and a long enlarged posterior part	*Stopractinca*

Nematoda: Dorylaimida: Longidoridae: Genera

1	Odonstostyle nonforked, odontophore without flanges, single guiding ring	2
1′	Odontostyle forked, odontophore with basal flanges, guiding ring double	*Xiphinema**
2(1)	Amphidial fovea stirrup shaped with wide slit opening	*Paralongidorus**
2′	Amphidial fovea pouch-like, amphidial opening a pore (difficult to observe; Fig. 9.3 F)	*Longidorus**

Nematoda: Dorylaimida: Aporcelaimidae: Genera

1	Odontostyle axial 2
1′	Odontostyle a mural tooth (on ventral wall, straight and parallel with stoma wall) ..... *Sectonema*
2(1)	Lip region strongly offset 3
2′	Lip region only slightly marked from the adjoining body ..... *Makatinus*
3(2)	Lip region without inner liplets; vulva with smooth cuticle 4
3′	Lips provided with inner liplets; vulva with wrinkled cuticle ..... *Epacrolaimus*
4(3)	Body length ≤4mm 5
4′	Body length 4−10mm; cuticle thick with crisscross fibers, lip region broad, tail shorter than anal body diameter ..... *Aporcelaimus*
5(4)	Males rare or uncommon; tail shape similar in both sexes, always short, conoid-rounded or hemispherical; body cuticle with two layers showing different refraction (outer transparent, inner compact); lip region sharply offset, not high; body clearly tapered toward anterior end ..... *Aporcelaimellus*
5′	Males usually common, tail similar conoid in both sexes and longer (up to twice anal diameter), cuticle moderately thick with fine transverse striae; lips sharply offset, high and narrow ..... *Metaporcelaimus*

Nematoda: Dorylaimida: Thorniidae: Genera

1	Spicules dorylaimoid (=arcuate with inner sclerotized septa; Fig. 9.6 D); only one precloacal ventromedian supplement ..... *Nygolaimoides*
1′	Spicules alaimoid (short straight, no inner sclerotization); no precloacal ventromedian supplements ..... *Thornia*

Nematoda: Dorylaimida: Nordiidae: Genera

1	Odontostyle not very thin, odontophore often flanged 2
1′	Odontostyle very thin and long (more than three times the labial width) odontophore bacilliform, never flanged ..... *Longidorella*
2(1)	Tail short, rounded or conoid in both sexes 3
2′	Tail long filiform in both sexes ..... *Lenonchium*
3(2)	No sclerotized platelets around stoma 4
3′	Sclerotized platelets around stoma ..... *Pungentus*
4(3)	Body cuticle near vulva smooth 5
4′	Body cuticle coarsely wrinkled anterior/posterior to vulva ..... *Rhyssocolpus*
5(4)	Odontophore with basal flanges; guiding ring double; lip region more or less offset; labial papillae prominent; tail hemispherical ..... *Enchodelus*
5′	Odontophore simple; guiding ring single; lip region offset; lips prominent; tail short conoid ..... *Dorydorella*

Nematoda: Dorylaimida: Dorylaimidae: Genera

1	Species with both sexes, odontostyle variable 2
1′	Only female known, odontostyle sinuate, vulva sunken ..... *Drepanodorylaimus*
2	Tail long, filiform in both sexes 3
2′	Tail different in male and female 5
3(2)	Prerectum shorter in both sexes (<4x anal body width in females); body less slender 4
3′	Prerectum very long in both sexes, >15X anal body diameter; body very slender (≤80x anal body diameter ..... *Protodorylaimus* (in part)
4(2)	Precloacal supplements not numerous (6−13), spaced ..... *Prodorylaimium*
4′	Precloacal supplements numerous (13−31), contiguous ..... *Protodorylaimus* (in part)
5(2)	Cuticle marked with longitudinal ridges 6
5′	Cuticle without longitudinal ridges 7
6(5)	Precloacal supplements arranged in continuous series ..... *Dorylaimus*
6′	Precloacal supplements in fascicles (Fig. 9.6 E) ..... *Ischiodorylaimus*

7(5)	Prerectum beginning about level anteriormost ventromedian precloacal supplements or within range of these supplements	8
7′	Prerectum, beginning far anterior to anteriormost ventromedian precloacal supplement	11
8(7)	Male tail short, rounded; guiding ring single or double	9
8′	Male tail conoid; guiding ring always single	10
9(8)	Guiding ring double	*Paradorylaimus*
9′	Guiding ring mostly single, seldom double	*Mesodorylaimus*
10(8)	Male conoid tail with pointed tip	*Afrodorylaimus*
10′	Male conoid tail with terminal peg	*Baladorylaimus*
11(7)	Cuticle smooth or finely striated	12
11′	Cuticle distinctly annulated	*Idiodorylaimus*
12(11)	No yellowish spots at odontostyle base; male tail short, bluntly rounded, straight	13
12′	Conspicuous yellowish spots around base of odontostyle; male tail conoid, rounded, ventrally bent	*Crocodorylaimus*
13(12)	Precloacal supplements contiguous, in a continuous row	14
13′	Precloacal supplements in two groups with some intermediate elements	*Calodorylaimus*
14(13)	Body very slender (a = 60−92); odontostyle weak, slender	*Chrysodorus*
14′	Body broader; odontostyle robust, strong and long	*Laimydorus*

Nematoda: Dorylaimida: Qudsianematidae: Genera

1	Numerous glandular cells and pores in lateral chords	2
1′	Lateral chords without such glands	4
2(1)	Lip region broad, strongly offset, with inner lips; odontostyle symmetrical, straight; vagina without sclerotization	3
2′	Lip region extremely narrow, unusual small head; odontostyle asymmetrical, dorsally bent, with very large aperture; vagina with sclerotization	*Paraxonchium*
3(2)	Labial region sucker-like (Fig. 9.4 H), much wider than adjacent body; tail bluntly rounded or conoid	*Discolaimus*
3′	Labial region not sucker-like, less widened; tail elongate (2−5 anal body diameters long)	*Discolaimoides*
4(1)	Lips well-developed, odontostyle robust with aperture about 1/3rd of its length; vagina sclerotized	5
4′	Lips fused; odontostyle slender with very small aperture; vagina not sclerotized	*Chrysonema*
5(4)	Female reproductive system didelphic	6
5′	Female reproductive system mono-opisthodelphic	*Ecumenicus*
6(5)	Distal part of tail with pseudocoel and not “empty” (=hyaline)	7
6′	Distal part of tail without pseudocoel, described as “empty”; one pair of ventrosublateral gland nuclei in pharynx	*Boreolaimus*
7(6)	Guiding ring simple, vulva mostly transverse, seldom longitudinal	8
7′	Guiding ring double, vulva longitudinal	*Arctidorylaimus*
8(6)	Tail rounded or bluntly rounded, about as long as anal diameter	9
8′	Tail conoid or convex−conoid, mostly distinctly longer, if shorter (1−3 anal diameters), tapered at its end, not broadly rounded	11
9(8)	Oral field ± sunken, inner liplets present	10
9′	Oral field not sunken, no inner liplets	*Crassolabium*
10(9)	Vulva a longitudinal slit; precloacal supplements contiguous	*Labronema*
10′	Vulva a transverse or longitudinal slit; precloacal supplements not contiguous	*Labronemella*
11(8)	Tail short (1−3 anal body diameters long)	12
11′	Tail comparatively long (4−8 anal diameters), female tail ventrally curved, male rare	*Epidorylaimus**
12(11)	Adcloacal and posterior most papillae not separated by a hiatus; most posterior midventral precloacal supplement in range of spicule or just anterior to it	13

12′	Precloacal hiatus present, most posterior midventral precloacal supplement well anterior to retracted spicule ..... *Eudorylaimus*
13(12)	Body small (<1 mm); pharynx about 1/3rd of body length and expanded posterior part of pharynx rather long (2/5th of total pharynx), males rare ..... *Microdorylaimus*
13'	Body longer; pharynx about 1/4th of body length; expanded pharynx part about 50% of its length; males common ..... *Allodorylaimus*

Nematoda: Triplonchida: Diphtherophorina: Families

1	Outer labial sensilla and four cephalic sensilla papilliform 2
1'	Outer labial sensilla setiform and longer than four setiform cephalic setae arranged in a single circlet; large protruding dorsal tooth ..... Odontolaimidae, one genus: *Odontolaimus*
2(1)	Complex tooth with basal knobs; cheilostom wall with thickened plates and refractive ring at base ..... **Diphtherophoridae**
2′	Onchiostyle composed of a tooth (onchium) on a dorsally curved support (onchiophore) (Fig. 9.2 D)..... **Trichodoridae**

Nematoda: Triplonchida: Diphtherophorina: Diphtherophoridae

1	Dorsal tooth aciculate ..... *Tylolaimophorus*
1′	Dorsal tooth shorter, appearing divided ..... *Diphtherophora*

Nematoda: Triplonchida: Diphtherophorina: Trichodoridae: Genera

1	Male without caudal alae; female with a well-developed vagina [about half corresponding body diameter (cbd) long] and well-developed sclerotized vaginal pieces ..... *Trichodorus*
1′	Male with caudal alae; female with short vagina (at most 1/3rd of cbd), vaginal sclerotized pieces little developed ..... *Paratrichodorus*

Nematoda: Triplonchida: Families

1	Amphidial aperture and fovea far posterior stoma; tail without caudal glands and spinneret 2
1′	Amphidial aperture and fovea at level of stoma; tail with caudal glands and spinneret 4
2(1)	Amphidial aperture a transverse slit (Fig. 9.3 H), fovea obscure pocket shaped; tail usually filiform 3
2′	Amphidial fovea unispiral, crescentiform, or round; tail conoid or subcylindrical ..... Triplonchida: **Bastianiidae**
3(2)	Stoma prismatic, cuticularized, with small dorsal tooth and two ventrosublateral tumid or radoform structures at stoma base; anterior labial sensilla papilliform, outer labial sensilla and cephalic sensilla setiform, arranged in two circlets; amphidial aperture a transverse slit ..... Tobrilina: Prismatolaimidae: one genus *Prismatolaimus*
3′	Stoma infundibuliform or cylindrical, with one large dorsal tooth or three large teeth (one dorsal and two ventrosublateral); anterior sensilla in two circlets, the outer labial and cephalic sensilla setiform; amphidial aperture slit-like ..... Tripylina: **Onchulidae**
4(1)	Stoma anteriorly infundibuliform or cylindriform, sclerotized, posteriorly with three stomatal pockets (one dorsal and one left ventrosublateral and one right ventrosublateral), the latter two usually well developed with a small tooth, the dorsal pocket poorly developed with one dorsal tooth; cardia surrounded by three large cardiac glands ..... Tobrilina: **Tobrilidae**
4′	Stoma narrowly infundibuliform, posterior part (pharyngostom) with dorsal tooth and two ventrosublateral denticles ..... Tripylina: **Tripylidae**

Triplonchida: Bastianiidae: Genera

1	Amphidial fovea unispiral (may show a thickened anterior border); tail conoid, tail tip with mucro; precloacal supplements small ..... *Bastiania*
1′	Amphidial fovea large round; tail bluntly rounded, tip devoid of mucro; precloacal supplements large ..... *Dintheria*

Triplonchida: Tripylina: Onchulidae: Genera

1 Stoma anteriorly wide, posteriorly narrow, and midway with three large teeth; cardia long (as long as or longer than body width) ..... *Stenonchulus*

1′ Stoma wide, with large dorsal tooth at mid-stoma and stoma base with 2−3 transverse folds; cardia shorter ..... *Onchulus*

Triplonchida: Tobrilina: Tobrilidae: Genera

1 Stoma large, with pockets and teeth (Fig. 9.4 I) 2

1′ Stoma shorter, poculiform, without pockets; teeth when present, very small ..... *Quasitobrilus*

2(1) Pharyngeal musculature encircling stoma; stoma variable, not cylindriform 3

2′ Pharyngeal musculature not encircling the stoma; stoma large, cylindriform with two minute denticles ..... *Kurikania*

3(2) At least one stomatal pocket is merged with anterior part of pharyngostom 4

3′ Stomatal pockets not merged with anterior part of pharyngostom 6

4(3) Stomatal pockets merged with anterior part of pharyngostom 5

4′ Only the anterior ventrosublateral stomatal pocket fused with wider anterior part of pharyngostom; spicules short ..... *Epitobrilus*

5(4) Pharyngostom spacious, thick-walled; two teeth well-developed; amphid aperture opposite posterior stoma ..... *Paratrilobus*

5′ Pharyngostom small, infundibuliform, thin-walled; two small teeth; amphid aperture more anteriorly, just posterior to insertion cephalic setae ..... *Mesotobrilus*

6(3) Body with few, thin setae; outer labial setae and cephalic setae in one circlet; precloacal supplements papilliform (Fig. 9.6 F) 7

6′ Body with numerous spine-like setae; outer labial setae and cephalic setae arranged in two separate circlets; male precloacal supplements minute ..... *Asperotobrilus*

7(6) Stoma ventrosublateral pockets at same level, connected to one another but clearly separated from wider anterior part of pharyngostom; vaginal sphincter muscle not conspicuously developed 8

7′ Stoma with two pockets (each with one tooth) situated longitudinally; teeth rather distant from each other; vaginal sphincter muscle strongly developed (Fig. 9.4 I) 9

8(7) Male precloacal supplements small, not protruding; cephalic setae usually about 1/3rd of head diameter long ..... *Tobrilus*

8′ Male precloacal supplements protruding; cephalic setae longer (40%−60% of head diameter) ..... *Eutobrilus*

9(7) Spicules long and thick; vaginal musculature strongly developed, vagina anteriorly directed ..... *Semitobrilus*

9′ Spicules long and thin; vaginal musculature moderately to strongly developed, appearing bulbous ..... *Neotobrilus*

Triplonchida: Tripylidae: Genera

1 Female reproductive system monodelphic-prodelphic 2

1′ Female reproductive system didelphic-amphidelphic 3

2(1) Stomatal chamber with a small prominent dorsal tooth and two ventrosublateral teeth/denticles in small pockets; anterior sensilla arranged in three circlets ..... *Tripylina*

2′ Stoma with minute denticles (not in pockets); anterior sensilla arranged in three circlets, with cephalic setae at greater distance from outer labial sensilla and with additional, thinner subcephalic setae ..... *Trischistoma*

3(1) Cephalic setae present; stoma with one or two chambers 4

3′ Cephalic setae absent; stoma a narrow funnel with a clear dorsal tooth and two small ventrosublateral teeth; no chambers (pockets) ..... *Tobrilia*

4(3) Body cuticle thick; anterior sensilla arranged in three circlets; stomatal chamber with two small denticles and slightly posteriorly a larger dorsal tooth; male supplements small, extending to near head region ..... *Tripyla*

4′ Body cuticle thin; anterior sensilla arranged in two circlets; anterior stomatal chamber with a dorsal tooth and posterior chamber with two ventrosublateral denticles; male supplements extending halfway pharyngeal region ..... *Tripylella*

Nematoda: Plectida: Aphanolaimidae: Genera

1	Amphidial fovea ventrally unispiral (Fig. 9.3 L), with or without central elevation; cheilostom undifferentiated 2
1′	Amphid opening small circular, fovea larger unispiral and subcuticular (apparent as two circles), cheilostom reinforced by six rhabdia ..... *Anonchus*
2(1)	Oral opening distinct, gymnostom heavily sclerotized 3
2′	Oral opening minute, gymnostom not sclerotized ..... *Aphanolaimus*
3(2)	Male gubernaculum arcuate and usually two types of precloacal supplements (alveolar and tubular), seldom only tubular; vagina with or without *pars refringens vaginae* ..... *Aphanonchus*
3′	Male gubernaculum rectangular or plate-like; alveolar supplements absent; vagina without *pars refringens vaginae* ... *Paraphanolaimus*

Nematoda: Monhysterida: Families

1	Stoma weakly sclerotized (exc. *Monhystrella*), without ribs and partially or completely surrounded by pharynx; ventral gland well developed or obscure or absent; tail either with or without terminal setae, but never with a terminal pore 2
1′	Stoma wide cylindrical or cylindriform, sclerotized, with longitudinal ribs, and only at base surrounded by pharynx; ventral gland always present, spinneret absent, but tail with terminal pore ..... Sphaerolaimidae, one genus: *Hofmaenneria*
2(1)	Female reproductive system monodelphic; stoma largely infundibuliform 3
2′	Female reproductive system didelphic. Stoma small and narrow (Fig. 9.4 O); only four cephalic sensilla setiform ..... Linhomoeidae: one genus *Terschellingia*
3(2)	Cuticle distinctly annulated or finely striated; six outer labial setae generally longer than four cephalic setae; cheilostom dome-like and posterior part stoma infundibuliform; one (anterior) ovary and anterior testis on left side of intestine, posterior testis (may be absent) on right side of intestine ..... **Xyalidae**
3′	Cuticle smooth under light microscope; stoma infundibuliform; 10 setae (six outer labial and four cephalic) fine; single ovary on right side of intestine ..... **Monhysteridae**

Nematoda: Monhysterida: Xyalidae: Genera

1	Inner labial sensilla papilliform or setiform, followed by a circle of 10−12 setae; males without complex supplements 2
1′	Inner labial sensilla setiform, followed by a circle of 14 relatively long setae (outer labial, cephalic and additional lateral setae); males with complex precloacal supplements ..... *Sacromarinema*
2(1)	Tail with at least two terminal setae, stoma conical, weakly sclerotized; vulva located at maximum 3/4th of body length from anterior end ..... *Daptonema*
2′	Tail without terminal setae; stoma not sclerotized (Fig. 9.4 Q); vulva at 2/3rd of body length from anterior end ..... *Theristus*

Nematoda: Monhysterida: Monhysteridae: Genera

1	Ovary outstretched 2
1′	Ovary reflexed; males unknown ..... *Sinanema*
2(1)	Body less slender (a up to 45) and shorter; cephalic setae shorter than one head width; somatic setae present or absent; stoma with or without denticles; tail variable in length/shape 3
2′	Body slender (a = 43−100) and 1.5−2.4 mm long; cephalic setae about one head width long; somatic setae lacking; stoma narrow, infundibuliform without denticles; long filiform tail ..... *Anguimonhystera*
3(2)	Vulva between 50% and 75% of body length from anterior end; tail variable 4
3′	Vulva far posterior, at 80% from anterior end; tail rather short, conical to elongate-conical ..... *Geomonhystera**
4(3)	Stoma subdivided with distinct denticle(s) 5
4′	Stoma simple, undivided, denticles mostly absent or obscure 6

5(4)	Posterior part of stoma (pharyngostome) with one small dorsal denticle; pharynx with basal bulb; vulva at midbody; female reproductive system usually very short; tail with extremely long spinneret ..... *Monhystrella*
5′	Pharyngostome with three minute denticles; pharynx largely cylindrical with slightly wider base; vulva posterior to mid-body (at 56%–70%); tail with spinneret, but not extremely long ..... *Tridentula*
6(4)	Body medium-sized (0.8–1.4 mm); amphidial fovea with anterior margin within 1–1.2 head widths from anterior end; distance vulva–anus longer than tail; crystalloids present ..... *Monhystera*
6′	Body often smaller than 0.8 mm; amphidial fovea with anterior margin usually more than one head width from anterior end; distance vulva–anus usually shorter than filiform tail; crystalloids absent ..... *Eumonhystera*

Nematoda: Mononchida: Families

1	Stoma large, strongly sclerotized with large tooth/teeth, with or without ventrosublateral ridges 2
1′	Stoma long cylindrical with at its base a small left ventrosublateral denticle ... Bathyodontina, Cryptonchidae, one genus: *Cryptonchus*
2(1)	Stoma tapered at base; cardia nontuberculate 3
2′	Stoma broad with flattened base; cardia with three tubercula (Fig. 9.4) ..... Anatonchina: **Anatonchidae**
3(2)	Dorsal tooth moderately sized, not unguliform, ventrosublateral denticles if present arranged in longitudinal rows ..... Mononchina: **Mononchidae**
3′	Dorsal tooth large (Fig. 9.4 B), unguliform, denticles largely arranged in transverse rows ..... Mononchina: **Mylonchulidae**

Nematoda: Mononchida: Anatonchina: Anatonchidae: Genera

1	Stoma with dorsal tooth and one or two pairs of ventrosublateral teeth 2
1′	Stoma with single dorsal tooth 3
2(1)	All three teeth retrorse, equal in size (Fig. 9.4 C) ..... *Anatonchus*
2′	Dorsal tooth anteriorly directed, two ventrosublateral teeth retrorse ..... *Miconchus*
3(1)	Stoma with dorsal tooth about mid-way, and two ventrosublateral ridges 4
3′	Stoma with dorsal tooth, at base of stoma; no other armature ..... *Iotonchus*
4(3)	Stoma with dorsal tooth opposite nondentated ventrosublateral ridges; no denticles present ..... *Jensenonchus*
4′	Stoma with dorsal tooth opposite two dentated ventrosublateral ridges and a group of denticles ..... *Prionchuloides*

Nematoda: Mononchida: Mononchina: Mononchidae: Genera

1	Stoma with single massive dorsal tooth, often with longitudinal ridges/denticles 2
1′	Stoma with three large teeth without longitudinal ridges/denticles ..... *Comiconchus*
2(1)	Both ventrosublateral walls with a denticulate longitudinal ridge 3
2′	Each ventrosublateral ridge nondenticulate 4
3(2)	Ventrosublateral ridge with a small tooth opposite dorsal tooth and a short transverse rib; short longitudinal ridge present; tail elongate ..... *Paramononchus*
3′	Entire ventrosublateral longitudinal ridges denticulate; tail short conical ..... *Prionchulus*
4(2)	Each ventrosublateral wall with a fine longitudinal ridge, no terminal spinneret 5
4′	Opposite single dorsal tooth, a thin transverse rib on each ventrosublateral wall; terminal spinneret ..... *Mononchus*
5(4)	Each ventrosublateral ridge inconspicuous, fading anteriorly ..... *Coomansus*
5′	Each ventrosublateral ridge conspicuous, anteriorly ending on a dentiform projection ..... *Clarkus*

Nematoda: Mononchida: Mylonchulidae: Genera

1	Ventrosublateral stoma walls with transverse rows of denticles, forming a rasp ..... *Mylonchulus*
1′	Short transverse rows of spherical denticles in line with dorsal tooth apex ..... *Granonchulus*

Nematoda: Enoplida: Families

1	No cephalic capsule and stoma without mandibles but with teeth or unarmed; caudal glands absent or in tail or extending precaudally 2
1′	Cephalic capsule present and stoma with solid mandibles with unguiform anterior end (Fig. 9.4 J); teeth shorter than mandibles; one tubular precloacal supplement in male; caudal glands extending precaudally ..... Enoplina, Enoplidae, one genus: *Enoploides*
2(1)	Stoma very small, almost nonexistent 3
2′	Stoma larger, armed with teeth or unarmed 5
3(2)	Body not extremely narrowing anteriorly; caudal glands absent 4
3′	Body very thin anteriorly, at low magnification head region difficult to differentiate from tail region; caudal glands present ..... Ironina: **Oxystomatidae**
4(3)	Anterior sensilla arranged in two circlets and papilliform; males monorchic ..... Alaimina: **Alaimidae**
4′	Only six outer labial setae visible; males diorchic ..... Andrassyiidae, one genus: *Malakhovia*
5(2)	Stoma not elongated, armed or unarmed 6
5′	Stoma elongated, anteriorly with three well-developed eversible hamulate teeth (Fig. 9.4 K) ..... Ironina, Ironidae, one genus: *Ironus*
6(5)	Stoma subdivided or not, armed with teeth 7
6′	Stoma large spacious and toothless ..... Enoplina, Anoplostomidae, one genus: *Anoplostoma*
7(6)	Stoma subdivided, teeth present 8
7′	Stoma not subdivided or with different chambers; teeth large, hollow, can be unequal (Fig. 9.4 P) ..... **Oncholaimidae**
8(7)	Stoma subdivided in two unequal parts, with three teeth and largest tooth ventrosublateral; male exceptionally without stoma ..... **Enchelidiidae**
8′	Stoma with several chambers, armed with teeth or cuticular projections; six outer labial setae longer than four cephalic setae ..... Tripyloidina, Tripyloididae, one genus: *Tripyloides*

Enoplida: Ironina: Oxystomatidae: Genera

1	Amphidial fovea not long longitudinal groove, aperture a transverse slit; female reproductive system monodelphic-opistodelphic 2
1′	Amphidial fovea a long longitudinal groove, aperture obscure, pore-like; female reproductive system didelphic ..... *Halalaimus*
2(1)	Amphidial fovea poculiform, located anterior to cephalic setae ..... *Thalassolaimus*
2′	Amphidial fovea oval, located posterior to cephalic setae ..... *Oxystomina*

Enoplida: Alaimina: Alaimidae: Genera

1	Amphid aperture incisiform to crescentiform 2
1′	Amphid aperture a pore, obscure ..... *Alaimus*
2(1)	Anterior sensilla arranged in two circlets 3
2′	Anterior sensilla, not protruding but receptors ending in puntiform cuticular indentations, anterior sensilla arranged in three circlets; amphid aperture incisiform with margins sclerotized; female reproductive system monodelphic/opisthodelphic, vulva lips sclerotized ... *Scleramphidelus*
3(2)	Amphidial aperture incisiform, fovea not oval to crescentiform; female reproductive system mostly didelphic amphidelphic; vagina thick, vulva open; male rare ..... *Amphidelus*
3′	Amphidial aperture large oval, crescentiform, fovea infundibuliform; female reproductive system monodelphic, opisthodelphic; vagina not thickened; vulva closed; amphidial fovea large oval to crescentiform; male rare ..... *Paramphidelus*

Enoplida: Alaimina: Andrassyidae: Genera

1	Stoma not developed; pharynx with posterior nonmuscular widening; uterus with hemirosette structure ..... *Andrassya*
1′	Stoma small but distinct, weakly sclerotized and unarmed; pharynx with posterior oval muscular widening; uterus without hemirosette structure ..... *Malakhovia*

Enoplida: Oncholaimina: Oncholaimidae: Genera

1 Stoma with left ventrosublateral tooth largest 2

1′ Stoma with right ventrosublateral tooth largest; female didelphic, demanian system well developed, with long main duct and terminal duct in anal region; main duct connected to intestine by *ductus entericus* and osmosium ..... *Adoncholaimus*

2(1) Female monodelphic/prodelphic with a developed demanian system ..... *Oncholaimus*

2′ Female monodelphic/prodelphic; demanian system absent ..... *Pseudoncholaimus*

Enoplida: Oncholaimina: Enchelidiidae: Genera

1 Amphidial fovea dorsally spiral; males with two well-developed, sclerotized poculiform precloacal supplements; stoma large, subdivided by several rows of denticles, three teeth, right ventrosublateral one largest and acute (Fig. 9.4 P) ..... *Eurystomina*

1′ Amphidial fovea not spiral (poculiform in female, oval in male); female stoma large and subdivided by a transverse ring or row of denticles in two unequal parts and provided with three slender teeth, one ventrosublateral largest and eversible; male without stoma ..... *Calyptronema*

Nematoda: Plectida: Families

1 Pharynx cylindrical or with basal bulb, S-E-pore located at level of nerve ring or more anteriorly 2

1′ Pharynx with median and basal widening, the latter without valves; secretory-excretory pore located at level of anterior intestine ..... Ohridiidae, one genus: *Domorganus*

2(1) Pharynx with radial tubes originating at base stoma; male usually with one pair of postcloacal papillae 3

2′ Pharynx without radial tubes and basal bulb without valve; stoma long tubular with well-developed stegostom; male usually with one pair of precloacal setae; postcloacal papillae absent ..... Leptolaimidae, one genus: *Paraplectonema*

3(2) Pharyngeal bulb terminal or slightly subterminal, possessing a complex valvular apparatus with transverse plates, smooth, denticulate or corrugated; posterior stegostom part short; female reproductive system didelphic 4

3′ Pharyngeal bulb subterminal, with denticulate ridges and a long muscular narrow basal part; posterior stegostom part long; amphidial fovea sellaeform or arcuate; female monodelphic, prodelphic ..... Chronogasteridae, one genus: *Chronogaster*

4(3) Lip region with distinctly divided lips with sclerotized edges; outer labial sensilla setiform; male with a single testis ..... **Metateratocephalidae**

4′ Lip region without distinctly divided lips; lips without sclerotized edges; outer labial sensilla papilliform; male with two testes ..... **Plectidae**

Plectida: Metateratocephalidae: Genera

1 Labial region coroniform, strongly offset; cheilostom with small sclerotizations; tail usually curved dorsad upon fixation; male with a small precloacal papilliform sensillum ..... *Metateratocephalus*

1′ Labial region lower, continuous with body contour; cheilostom without sclerotizations; tail usually curved ventrad; male with large precloacal papilliform sensillum ..... *Euteratocephalus*

Plectida: Plectidae: Genera

1 Anterior end with distinct cervical expansions 2

1′ Anterior end without cervical expansions; lip region different 3

2(1) Cervical cuticular expansions annulated, a series of 9–13 annulae, extending posteriorly to subcephalic setae; cephalic setae modified (cornua), i.e., flattened, foliform with finely rounded terminus ..... *Tylocephalus*

2′ Cervical cuticular expansions bulbiform, not annulated; each expansion extends anteriorly into a long median fimbrate flagellum; cephalic sensilla strongly modified into triangular cornua ..... *Wilsonema*

3(1)	Somatic setae present over the whole body; amphidial fovea unispiral (Fig. 9.3 I)	*Plectus*
2′	Somatic setae restricted to tail; amphidial aperture a transverse slit	*Anaplectus*

Nematoda: Chromadorida: Families

1	Amphidial fovea round to circular, uni- to multispiral turns, always distinct in LM and located clearly posterior to cephalic setae	2
1′	Amphidial fovea transverse oval-shaped ventrally spiral, usually hardly visible and located far anteriorly on head	**Chromadoridae**
2(1)	Anterior pharynx (pharyngostom) not enlarged; outer labial sensilla arranged in one circlet together with four cephalic setae; amphidial fovea multispiral	3
2′	Anterior pharynx (pharyngostom) enlarged (Fig. 9.5 C); four cephalic setae arranged in a third circlet of anterior sensilla; amphidial fovea circular to unispiral	Ethmolaimidae, one genus: *Ethmolaimus*
3(2)	Pharynx with moderately developed end bulb; both gonads (ovaries/testes) on same side of the intestine (left or right)	Achromadoridae, one genus: *Achromadora*
3′	Pharynx at base enlarged but without well-developed end bulb; both gonads on different sides of the intestine	Cyatholaimidae, one genus: *Paracyatholaimus*

Nematoda: Chromadorida: Chromadoridae: Genera

1	Pharynx a double posterior bulb	2
1′	Pharynx a single (± developed) posterior bulb	3
2(1)	Cuticle ornamentation with two rows or larger dots (Fig. 9.3 C); labial region usually offset and narrower; anterior pharynx dorsally swollen in association with dorsal tooth; tail without very long spinneret	*Ptycholaimellus*
2′	Cuticle ornamentation with more than two rows of larger dots, labial region not narrower; pharynx anterior slightly and nearly symmetrically swollen; tail with extremely long spinneret	*Spilophorella*
3(2)	Tooth or teeth hollow	4
3′	Teeth solid	6
4(3)	Pharynx anteriorly enlarged; body cuticle either with slightly more pronounced punctation laterally or lateral differentiation with 2–3 rows of large dots	5
4′	Pharynx anteriorly not enlarged; smooth lateral field flanked by two longitudinal rows of large dots	*Dichromadora*
5(4)	Cuticle complex heterogeneous with lateral differentiation well expressed with 2–3 rows of large dots	*Neochromadora*
5′	Cuticle homogeneous with lateral differentiation less distinct, only as slightly more pronounced punctation, no distinct rows of larger dots	*Chromadorita*
6(3)	Cuticle punctation homogeneous, without (obvious) lateral differentiation	7
6′	Cuticle punctation with lateral dots bigger than submedian dots	*Punctodora*
7(6)	Three nearly equally sized solid teeth; ocelli may be present	*Chromadorina*
7′	A single large dorsal tooth opposed to a ventrosublateral pit or elevation or two small ventrosublateral teeth	*Prochromadora*

Nematoda: Araeolaimida: Families

1	Stoma long but unarmed	Diplopeltidae, one genus: *Cylindrolaimus*
1′	Stoma long cylindrical and armed with three small teeth	**Rhabdolaimidae**

Nematoda: Araeolaimida: Rhabdolaimidae: Genera

1	Pharynx with well-developed end bulb with a simple valve; ovaries reflexed	*Rhabdolaimus*
1′	Pharynx with a slight terminal swelling, no valve; ovaries outstretched	*Rogerus*

Nematoda: Desmodorida: Families

1	Body cuticle annulated; amphidial fovea spiral 2
1′	Body cuticle smooth; amphidial aperture incisiform, fovea poculiform ..... *incertae sedies*, one genus: *Udonchus*
2(1)	Head not offset, not swollen; amphidial fovea cryptospiral; ovary reflexed ..... Desmodoridae, one genus: *Prodesmodora*
2′	Head swollen; amphidial fovea unispiral, circular in outline; ovaries outstretched ..... Microlaimidae, one genus: *Microlaimus*

Nematoda: Rhabditida: Suborders *Sensu* Andrássy (2005)

1	Lip region without probolae or processes; basal bulb pharynx nonvalvate or valvate female reproductive system didelphic or monodelphic; male with or without bursa 2
1′	Lip region usually with complex processes (probolae); stoma narrow but anterior part can be wide, unarmed or sometimes with small denticles; stegostom comprises 2/3rd or more of stoma length; pharynx corpus cylindrical without median bulb, isthmus thin and basal bulb rounded valvate; female mono-prodelphic with ovary directed posteriad with double flexure near germinal zone; male without bursa, typically with 2−3 pairs of precloacal papillae and five pairs of caudal papillae ..... **Cephalobina**
2(1)	Stoma wide, armed with teeth (tooth; basal bulb nonvalvate; amphidial aperture often large, located postlabially 3
2′	Stoma tubular, with denticle in metastegostom; basal pharyngeal bulb with valve; amphid aperture pore-like and located on lips ..... **Rhabditina**
3(2)	Male without spicules but with a bursa ..... Myolaimina, one genus: *Myolaimus*
3′	Spicules present, bursa if present, weakly developed ..... **Diplogastrina**

Nematoda: Rhabditida: Diplogastrina: Families

1	Stoma not styliform 2
1′	Stoma styliform but composed of a short cheilostom and gymnostom, and a long tubular stegostom perradially flanked by apodemes pointing dorsally at the posterior end and with a movable dorsal and a right ventrosublateral tooth that cross each other (Fig. 9.5 M) ... Tylopharyngidae, one genus: *Tylopharynx*
2(1)	Gymnostom rather spacious and maximum twice as long as wide; stegostom with larger teeth 3
2′	Stoma cylindrical with gymnostom, 3−6 times as long as wide and (meta)stegostom with small denticles (=glottoid apparatus, Fig. 9.5 J–L) ..... **Diplogasteroididae**
3(2)	Dorsal tooth and right ventrosublateral tooth movable and unguiform, while left ventrosublateral side with plain or serrated plates; stegostom often elongated ..... **Neodiplogastridae**
3′	Dorsal tooth not movable, laminiform or setiform; ventrosublateral armature similar on right and left side, stegostom short ..... **Diplogastridae**

Nematoda: Rhabditida: Diplogastrina: Diplogasteroididae: Genera

1	Amphidial aperture large, oval, clearly visible, located opposite or more posterior to stoma; stegostom without lamellar process 2
1′	Amphid aperture a pore, located on posterior margins of lateral lips; stegostom with lamellar dorsal process with denticle; female reproductive system amphidelphic ..... *Rhabditidoides*
2(1)	Amphidial aperture wider than stoma and located opposite posterior stoma; metastegostom with minute denticle(s); median pharyngeal bulb weak, posterior part pharynx usually as long as anterior corpus; female reproductive system didelphic, vulva anterior to midbody; spicules short, hardly bent ..... *Goffartia*
2′	Amphidial aperture slightly smaller; metastegostom with small dorsal tooth; posterior part of pharynx shorter than anterior corpus with spherical median bulb (metacorpus); female reproductive system prodelphic, vulva near midbody; spicules arcuate .... *Diplogasteroides*

Nematoda: Rhabditida: Diplogastrina: Diplogastridae: Genera

1	Female reproductive system didelphic	2
1′	Female reproductive system monodelphic–prodelphic	*Acrostichus*
2(1)	Uterus with a separate dorsal pouch at level of vulva	*Diplogasteritus*
2′	Uterus without a separate dorsal pouch	3
3(2)	Outer labial sensilla papilliform or short setiform papilla	4
3′	Outer labial sensilla setiform, and elongate	*Butlerius*
4(3)	Cheilostom wall longitudinally divided into platelets; dorsal tooth small, ventrosublateral armature consisting of fine warts	*Paroigolaimella*
4′	Cheilostom wall not divided into platelets; gymnostom with oblique transverse folds; dorsal tooth large triangular	*Diplogaster*

Nematoda: Rhabditida: Diplogastrina: Neodiplogastridae: Genera

1	Stoma differentiated in a wider anterior part (cheilostom) and a narrower, longer posterior part (stegostom)	2
1′	Stoma with a spacious anterior cheilostom and gymnostom and a shorter, narrower stegostom	4
2(1)	Stegostom longer cylindrical	3
2′	Stegostom short cylindrical with two subdorsal apodemes, and anteriorly with an unguiform dorsal tooth, a right ventrosublateral tooth and a left ventrosublateral serrated plate	*Koernia*
3(2)	Stegostom long, cylindrical, with two alate subdorsal apodemes, posteriorly protruding	*Neodiplogaster*
3′	Stegostom without alate thickenings (Figs. 9.4 N and 9.5 G)	*Mononchoides*
4(1)	Stoma with left ventrosublateral plate smooth, nonserrated; gubernaculum very thick	*Oigolaimella*
4′	Stoma with serrated left ventrosublateral plate; gubernaculum simple, not thickened	*Fictor*

Nematoda: Rhabditida: Cephalobina: Families

1	Stoma rather spacious (cheilostom and gymnostom wider than stegostom)	**Panagrolaimidae**
1′	Stoma narrow (cheilostom widest part); cephalic and labial probolae generally present	**Cephalobidae**

Nematoda: Rhabditida: Cephalobina: Panagrolaimidae: Genera

1	Gymnostom well developed, as long as or longer than cheilostom	2
1′	Gymnostom much shorter than cheilostom; spicules with hamulate anterior end	*Panagrellus*
2(1)	Ovary far postvulvally reflexed; vulva lips protruding; spicules simple, arcuate	3
2′	Ovary not postvulvally reflexed; spicule sinuate	*Turbatrix*
3(2)	Body very slender (a = 30–70); vulval lips not protruding	*Propanagrolaimus*
3′	Body not slender (a = 14–30); vulval lips protruding	*Panagrolaimus*

Nematoda: Rhabditida: Cephalobina: Cephalobidae: Genera

1	Labial and cephalic probolae, if present, simple, low, generally hexaradiate	2
1′	Labial probolae high and more complicated; cephalic probolae mostly complicated, often very large	4
2(1)	Six lips or apparently four (lateral lips reduced), labial field hexaradiate or bilaterally symmetrical	3
2′	Three lips, labial region triradiate symmetrical; labial probolae low, asymmetrical; cephalic probolae, if present, minute	*Cephalobus*
3(2)	Cephalic probolae absent	*Eucephalobus*

3′	Cephalic propolae present, variable, stipulate to setiform	*Pseudacrobeles*
4(1)	Labial probolae bifurcate, each consisting of a shaft and two diverging arms	5
4′	Labial probolae simple, not sharp, shorter than lip region width	*Acrobeloides*
5(4)	Labial probolae not fringed; membranous tines, if present, less than 10, cephalic probolae smaller	6
5′	Labial probolae fringed (with at least 20 membranous tines) and as long or longer than lip region width; cephalic probolae fairly long triangular (Fig. 9.3 M)	*Acrobeles*
6(5)	Labial probolae smooth Y-shaped with thin shafts and branches of probolae shorter than shafts; cephalic probolae setose; pharyngeal corpus not swollen	*Cervidellus**
6′	Labial probolae biacute or bifurcate with broad shafts; cephalic probolae small, generally with two incisures	*Chiloplacus*

Nematoda: Rhabditina: Families

1	Body symmetrical	2
1′	Body asymmetrical	**Bunonematidae**
2(1)	Lip region radial symmetrical, without hook-like structures	3
2(1)	Lip region bilateral symmetrical, dorsal and ventral lips hamulate and strongly sclerotized ..	Diploscapteridae, one genus: *Diploscapter*
3(2)	Female reproductive system didelphic, vulva near midbody	4
3′	Female reproductive system monodelphic−prodelphic, vulva far posteriorly	**Mesorhabditidae**
4(3)	Bursa peloderan (enveloping tail tip)	5
4′	Bursa leptoderan (not enveloping tail tip)	**Rhabditidae**
5(4)	Metastegostom with well-developed glottoid apparatus (Fig. 9.2 A)	**Peloderidae**
5′	Metastegostom without glottoid apparatus	Protorhabditidae, one genus: *Protorhabditidis*

Nematoda: Rhabditida: Rhabditina: Bunonematidae: Genera

1	large scutiform fields present between the warts on right body side	*Craspedonema*
1′	No scutiform fields present	*Bunonema*

Nematoda: Rhabditida: Rhabditina: Mesorhabditidae: Genera

1	Bursa wall well developed, broad, peloderan (enveloping tail tip); male tail short	2
1′	Bursa less developed either narrow reduced and leptoderan (not enveloping tail tip) or wider and restricted to cloacal region; male tail elongate conoid	*Bursilla*
2(1)	Anterior sensilla papilliform. Spicules separate	*Cruznema*
2′	Anterior sensilla setiform papillae. Spicules fused from proximal tip over 1/3rd of their length	*Mesorhabditis*

Nematoda: Rhabditida: Rhabditina: Rhabditidae: Genera

1	Stegostom without dentiform projection; metastegostom iso- or anisoglottoid (Figs. 9.5 J, K)	2
1′	Stegostom with strong dentiform projection and at base metastegostom isoglottoid (Fig. 9.5 J); male with three pairs of precloacal papillae	*Cephaloboides*
2(1)	Stomatal tubular part at least twice as long as wide	3
2′	Stomatal tubular part maximum 1.5 times as long as wide	*Oscheius*
3(2)	Lips papillae without bristles	4
3′	Lips with bundles of fine bristles	*Rhabditoides*
4(3)	Bursal papillae (=rays, Fig. 9.6 I): anteriormost pair close to the others	5

4′	Bursal papillae: anteriormost pair far anterior to others	*Cuticularia*
5(4)	Metastegostom isomorphic (Fig. 9.5 J)	6
5′	Metastegostom anisomorphic (Fig. 9.5 K)	7
6(5)	Female tail conoid to filiform; spicule simple	*Rhabditis*
6′	Female tail cupola-shaped; each spicule with a long dorsal thorn	*Curviditis*
7(5)	Bursal genital papillae (rays) with seven pairs only, female tail conical or convex; spicules simple	*Poikilolaimus*
7′	Bursal genital papillae with (nine) 10 pairs; tail in both sexes conoid to elongate	*Rhabditella*

Nematoda: Rhabditida: Rhabditina: Peloderidae: Genera

1	Spicules separate, not fused	2
1′	Spicules fused to various degree; lips clearly separated	*Pelodera*
2(1)	Bursa open; lips separate; metastegostom isoglottoid with minute warts	*Pellioditis*
2′	Bursa anteriorly closed, sucker-shaped (Fig. 9.6 I); lips hardly separate; metastegostom isoglottoid with bristle-like denticles	*Caenorhabditis*

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Chapter 10

Phylum Nematomorpha

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INTRODUCTION

At least 159 species of freshwater horsehair worms (Nematomorpha, Gordiida) in 13 genera are known from the Palaearctic. They are parasitic on insects (mostly grasshoppers, crickets, and beetles) and emerge from the host at maturity. The typically terrestrial host is driven toward water, where the horsehair worm is released. Reproduction takes place in the water, and the tiny and morphologically distinct larvae infect intermediate (paratenic) hosts. Although relatively little is known about the gordiid life cycle, it seems that in general the intermediate host (e.g., mosquitos, mayflies) spans the gap between the aquatic and the terrestrial environment. Recent reviews were published by Hanelt et al. (2005) and Schmidt-Rhaesa (2013).

LIMITATIONS

Sexes can be distinguished using a hand lens, but specific determinations require a microscope. The female cloacal opening is always terminal on the rounded posterior end, with the exception of *Paragordius*, where the posterior end has three lobes and the cloacal opening is between these lobes. The male cloacal opening is always ventral and subterminal. Most Palaearctic species have two tail lobes posterior of the cloacal opening; however, representatives of a few genera have no tail lobes, but still possess a ventral cloacal opening. *Gordius* can be recognized by a semicircular fold called the postcloacal crescent.

Gordiids are sometimes confused with large nematodes in the Mermithida. In the immature, whitish stages, these taxa are indistinguishable. Some hints for distinction are a usually darker color in gordiids, pointed (Mermithida) versus rounded (Gordiida) body ends, the presence of tail lobes (some Gordiida) or the presence of a white anterior tip followed by a dark brown ring (Gordiida) (Fig. 10.1 B). In addition, mermithids are usually transparent in transmitted light, whereas gordiids will appear opaque due to their thick layering of cuticle.

Proper specific determination requires higher magnifying techniques. A superficial cuticle sample with removed musculature gives a good impression of the surface structure and especially on the pattern of structures called areoles. Nevertheless, scanning electron microscopy has become the standard tool for gordiid determination, as fine structures can be observed reliably. This method is necessary for a certain identification of most species.

One problem is that the significance of intraspecific morphological character variation is not well understood. In practice this means that it is not clear whether minute morphological differences among specimens are due to intraspecific variation or are indications for separate species.

In the parasitic stage, gordiids can usually not be determined morphologically. Due to the parasitic life style, the free-living adult stage is seasonal and rarely found. As gordiid larvae encyst in a variety of paratenic hosts, a host tissue search may yield cysts. Encysted larvae of the three most common Nearctic species can be distinguished

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morphologically, but comparable work for Palaearctic larvae is not available.

TERMINOLOGY AND MORPHOLOGY

Gordiids (Fig. 10.1 A) have comparably few diagnostic characters. At the anterior end, the shape (distinctly tapering or stouter) as well as the coloration is important. The anterior tip is usually whitish (Fig. 10.1 B) and in several species this is followed by a dark brown or black ring often called a **dark collar**. A ventral and probably also a dorsal longitudinal line of darker coloration may be present. At the posterior end, **tail lobes** can be present in females of *Paragordius* (Fig. 10.2 A) and in males of *Gordius*, *Paragordius*, *Gordionus, Parachordodes, Paragordionus, Acutogordius, Progordius, Digordius,* and *Semigordionus* (Figs. 10.2 B, F). The single opening in the posterior end leads into the intestinal tract as well as to the gonads and is, therefore, a cloacal opening. The **postcloacal crescent** is a semicircular fold posterior to the male cloacal opening (Fig. 10.2 B), and is characteristic for *Gordius* and *Acutogordius*. Other male posterior end structures include **cuticular bristles** or **conical spines** (Fig. 10.2 C). In some species, such structures are clustered. Spines scattered on the tail lobe medial surfaces are called **postcloacal spines** (Fig. 10.2 C). **Precloacal bristlefields** may be present on the tail lobes, on the entire ventral side of the posterior end, or in the anterolateral rows of the cloacal opening (Fig. 10.2 C).

The cuticle is smooth in a few species, but structured into regular elevations in others (Figs. 10.3 A–G). Such elevations are called **areoles**. The areoles terminology follows Schmidt-Rhaesa et al. (2008). Areoles may be present as polygonal structures covering the entire cuticle (Fig. 10.3 A). They are separated by grooves, in which interareolar structures may be present. In *Parachordodes*, *Paragordionus*, *Chordodes*, *Euchordodes*, *Spinochordodes,* and *Lanochordodes*, two or more areole types are present (Fig. 10.3 B). In *Paragordionus*, where smaller and larger areoles are present, the larger ones are called **megareoles** (Fig. 10.3 B), and they form clusters among the smaller areoles. In *Parachordodes*, even larger areoles are present, which are probably the products of several fused megareoles, and are called **superareoles** (Fig. 10.3 C). In

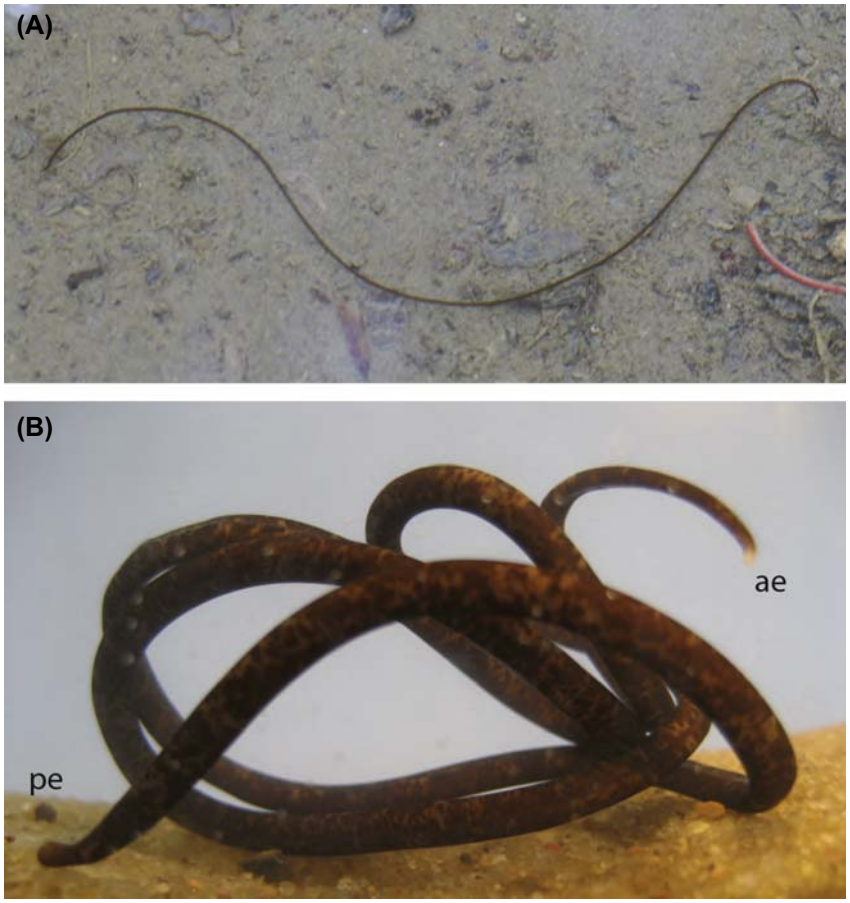


FIGURE 10.1 (A) Living gordiid in its habitat, a shallow puddle in Swizerland (photograph by Axel Groenfeld); and (B) undetermined specimen from the genus *Chordodes* with whitish anterior tip (ae) and broader posterior end (pe).

Chordodes, elevated areoles with an apical "crown" of short or long bristles are present (Figs. 10.3 D, E). This type of areole is called a "crown areole." Other types of areoles present in the cuticle of *Chordodes* are simple areoles, **tubercle areoles**, **thorn areoles**, **circumcluster areoles,** and **bulging areoles** (see Figs. 10.3 D, E). Bulging areoles are not figured here; they are clearly elevated areoles among the simple areoles. The terminology of these areoles follows Schmidt-Rhaesa et al. (2008).

MATERIAL PREPARATION AND PRESERVATION

Nematomorphs are best preserved in 70% ethanol, except for DNA work, for which material should be preserved in 100% ethanol and placed in a freezer. Follow the usual protocols of dehydration, critical point drying, and sputtering for scanning electron microscopy. For light microscopy, cuticular samples can either be removed by a tangential section with a razor blade when the worm is stretched or by cutting a complete section from the mid-body region. This section (length about 1 mm) is cut longitudinally and internal tissue is scraped off with a scalpel. Then, the cuticle can be observed on a slide either in ethanol or, preferably, after transfer into glycerol.

KEYS TO GORDIIDA

Gordiida: Gender

1	Ventral cloacal opening (Figs. 10.2 B–E)	**males**
1′	Terminal cloacal opening (except *Paragordius*, where the cloacal opening is in between the lobes)	**females**

Gordiida Males: Genera

1	Paired tail lobes present (Fig. 10.2 A)	2
1′	Tail lobes absent, posterior end rounded (Figs. 10.2 B, D, F)	7
2(1)	Postcloacal crescent present (Fig. 10.2 B)	3
2′	Postcloacal crescent absent (Fig. 10.2 C)	4
3(2)	Tail lobes rounded apically (Fig. 10.2 B) [Genus in need of revision]	*Gordius*
3′	Tail lobes pointed apically	*Acutogordius obesus* Camerano, 1895 (one Palaearctic species with questionable geographic assignment, only males known)
4(2)	Tail lobes shorter than twice the width of one lobe (Figs. 10.2 B, C, F)	5
4′	Tail lobes longer than twice the width of one lobe (Fig. 10.2 E) [*Digordius* and *Progordius* are poorly described and in need of revision]	***Paragordius***/*Digordius*/*Progordius*
5(4)	Areoles of multiple types present (Fig. 10.3 B)	6
5′	Areoles of a single type (Fig. 10.3 A) [*Gordionus* is in need of revision, the single species *S. circumannulatus* Heinze, 1952 may belong to *Gordionus*]	*Gordionus*/*Semigordionus*
6(5)	Larger areoles (megareoles) in clusters (Fig. 10.3 B)	***Paragordionus***
6′	Very large areoles with an apical pore (superareoles) present (Fig. 10.3 C) [Genus in need of revision]	*Parachordodes*
7(2)	Crown areoles absent (Figs. 10.3 C, D)	8
7′	Crown areoles present (Fig. 10.3 B)	***Chordodes***
8(7)	Two types of areoles forming cuticular patches (Fig. 10.3 F) [several poorly described species in *Spinochordodes*, one species in *Lanochordodes* (*L. zeravshanicus* Kirjanova, 1950), genera in need of revision]	*Spinochordodes*/*Lanochordodes*
8′	Areoles not in patches [Genus in need of revision]	*Euchordodes*

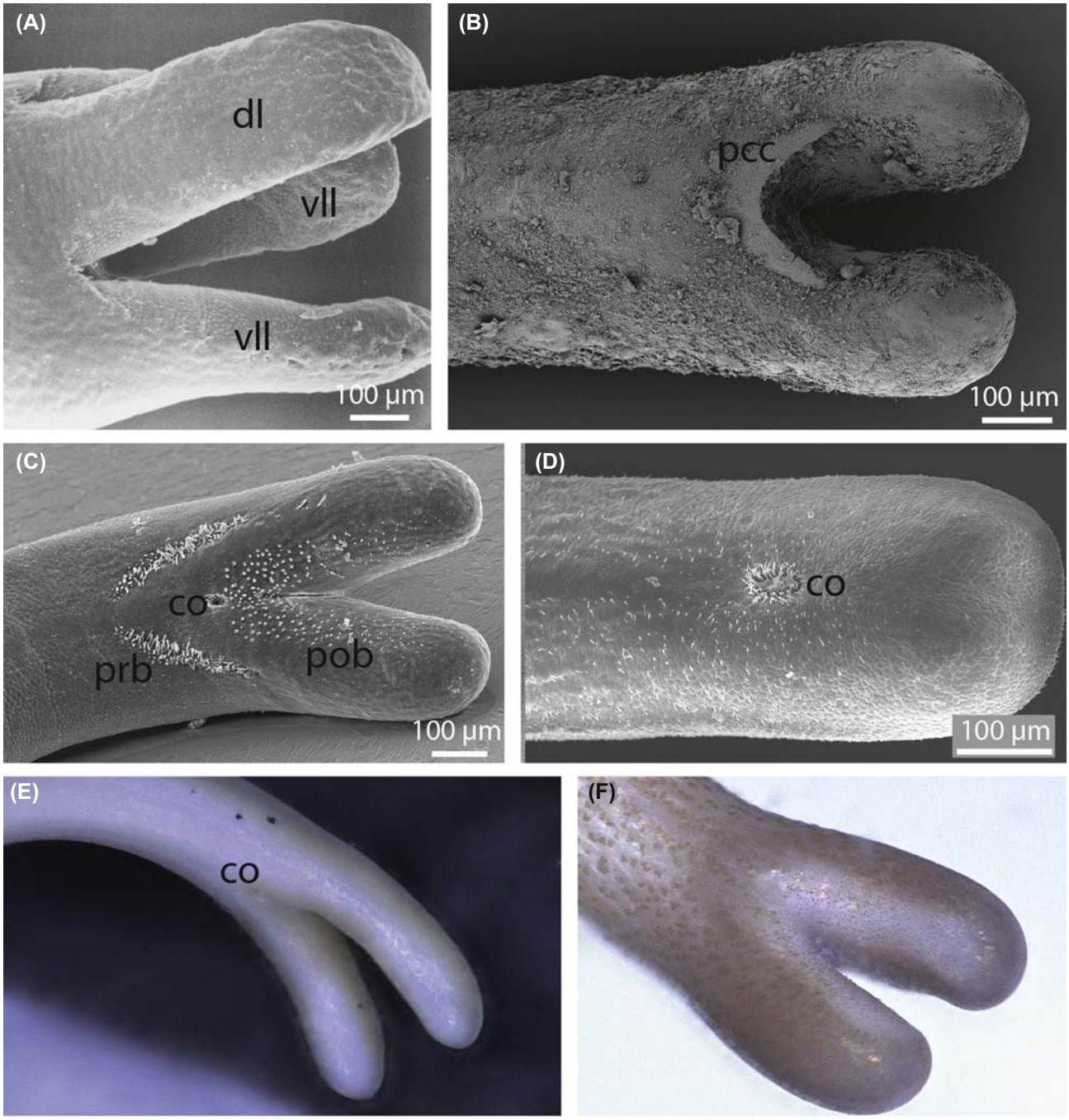


FIGURE 10.2 Shape of posterior ends of female (A) and males (B–F). All views on male posterior ends are from ventral. (A) *Paragordius varius* female with three lobes, one dorsal (dl) and two larger ventrolateral ones (vll); (B) *Gordius aquaticus* with postcloacal crescent (pcc); (C) *Gordionus violaceus* with cloacal opening (co), precloacal bristles (prb), and postcloacal bristles (pob); (D) *Spinochordodes tellinii* with no tail lobes; (E) *Paragordius tricuspidatus* with very long tail lobes; and (F) *Parachordodes* sp. A–D with SEM.

Gordiida Females: Genera

1	Posterior end rounded	2
1′	Three tail lobes present (Fig. 10.2 A)	***Paragordius***
2(1)	Cuticle with areoles	3
2′	Cuticle smooth [many poorly described species, genus in need of revision]	*Gordius*
3(2)	Crown areoles absent	4
3′	Crown areoles present (Fig. 10.3 D)	***Chordodes***
4(3)	More than one type of areoles present	5
4′	Only one type of areole present	*Gordius*/*Gordionus*/*Euchordodes*
5(4)	Larger areoles without an apical pore	6
5′	Very large areoles (superareoles) with an apical pore (Fig. 10.3 C)	*Parachordodes*
6(5)	Larger areoles (megareoles) in clusters (Fig. 10.3 B)	***Paragordionus***
6′	Two types of areoles forming cuticular patches (Fig. 10.3 F)	*Spinochordodes*/*Lanochordodes*

Gordiida: *Paragordius*: Species

1	Ventral cloacal opening (Figs. 10.2 B–E): males	2
1′	Terminal cloacal opening: females	3
2(1)	Paired row of small spines extends on the ventral side of the posterior end onto the tail lobes [Europe]	*Paragordius tricuspidatus* (Dufour, 1828)
2′	Entire ventral side of tail lobes covered with small spines [Europe, Turkestan]	*Paragordius stylosus* (Von Linstow, 1883)
3(1)	Dorsal tail lobe as long as lateral ones	*Paragordius tricuspidatus* (Dufour, 1828)
3′	Dorsal tail lobe shorter than lateral ones	*Paragordius stylosus* (Von Linstow, 1883)

Gordiida: *Paragordionus*: Species

All *Paragordionus* occur exclusively in the Palaearctic. Characteristic is the presence of two types of areoles, the larger megareoles form clusters of at least two areoles (Fig. 10.3 B). The maximum number of megareoles per cluster is important for species determination. However, most descriptions are based on few specimens and some variation may exist (see, e.g., Schmidt-Rhaesa & Wagner, 2013).

1	Number of megareoles 2–3 (Fig. 10.2 B)	2
1′	Number of megareoles >3	3
2(1)	Megareoles with surface smooth [Czech Republic]	*Paragordionus bohemicus* Havlik, 1947
2′	Megareole surface with marginal ring of knobs [Spain]	*Paragordionus ibericus* Schmidt-Rhaesa & Cieslak, 2008
3(1)	Number of megareoles >5	4
3′	Number of megareoles 3–4 [Japan]	*Paragordionus kawamurai* Yamaguti, 1943
4(3)	Number of megareoles 5–10 [Germany]	*Paragordionus dispar* (Müller, 1926)
4′	Number of megareoles >10 [Germany, probably Czech Republic]	*Paragordionus vejdovskyi* (Janda, 1894)

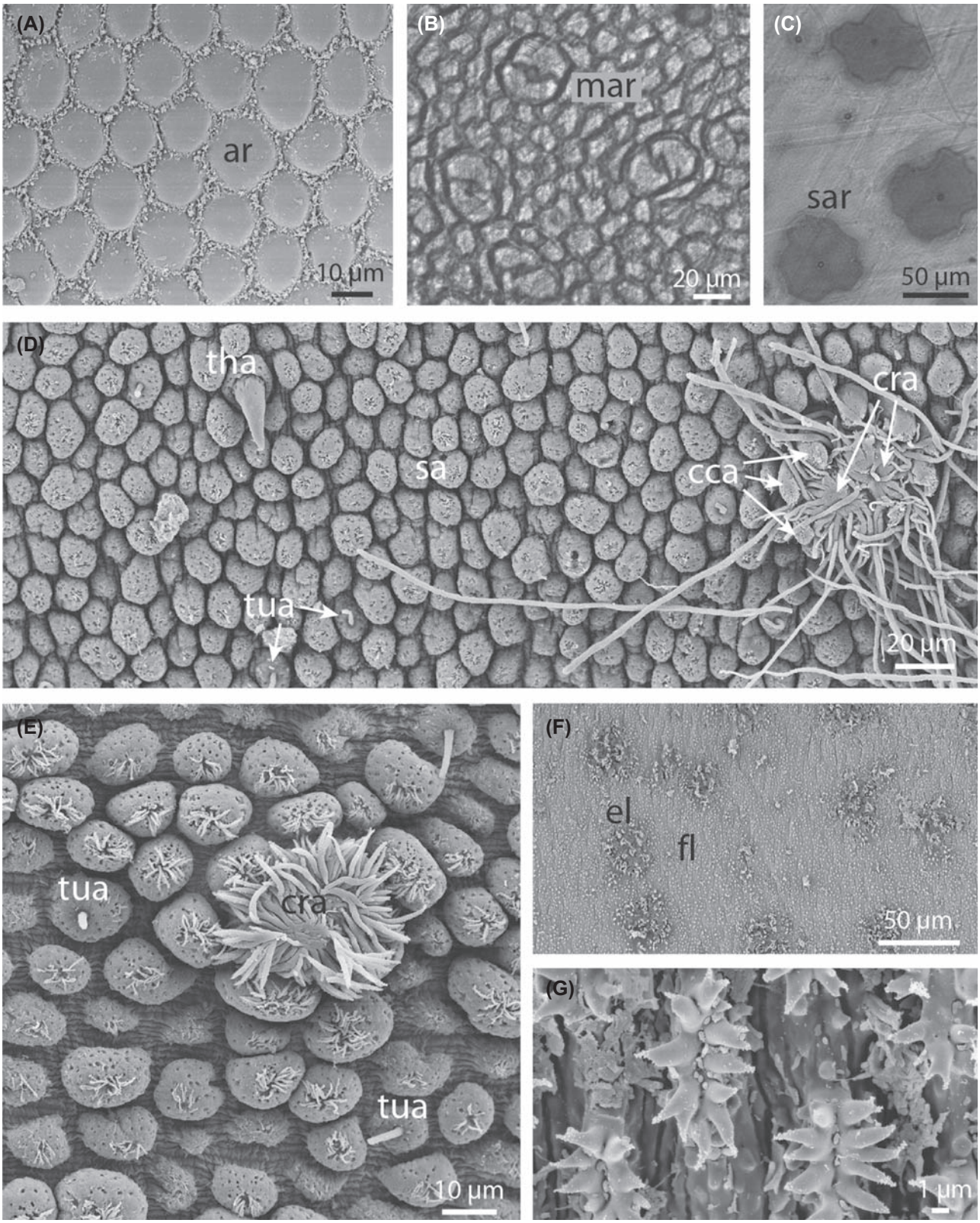


FIGURE 10.3 Areoles on the cuticular surface: (A) one type of flat areoles (ar) and interareolar structures in *Gordionus violaceus*; (B) small clusters of megareoles (mar) in *Paragordionus dispar* (larger clusters are also present in this species); (C) superareoles (sar) in *Parachordodes* sp.; (D) *Chordodes japonensis* with different types of areoles: simple areoles (sar), thorn areoles (tha), tubercle areoles (tua), crown areoles (cra), and circumcluster areoles (cca). Crown areoles are from the ventral midline and have very long apical filaments; (E) crown areoles from lateral body side of *C. japonensis* with shorter filaments; (F) patches of elevated (el) among flat (fl) areoles in *Spinochordodes tellinii*; and (G) magnification of elevated structures from image (F). All images as SEM.

Gordiida: *Chordodes*: Species

Chordodes is a large genus with 98 species (Schmidt-Rhaesa et al., 2008). The main distribution is tropical and subtropical, but 15 species are reported from the Palaearctic, 5 of which are insufficiently described.

1	Simple areoles present	2
1′	Simple areoles absent, tubercle areoles abundant	*Chordodes devius* Kirjanova, 1950 [Tajikistan]
2(1)	Crown areoles on entire surface	3
2′	Crown areoles only along ventral midline	*Chordodes sajanensis* Spiridonov, 2000 [Russia]
3(2)	Crown areoles in pairs, surrounded by circumcluster areoles (Fig. 10.3 D)	4
3′	Crown areoles in larger clusters (>two areoles), no circumcluster areoles	*Chordodes fukuii* Inoue, 1951 [Japan]
4(3)	Simple areoles with warty surface	5
4′	Simple areoles with more or less smooth surface	6
5(4)	Bulging areoles absent	*Chordodes silvestri* Camerano, 1895 [Japan]
5′	Bulging areoles present	*Chordodes koreensis* Baek, 1993 [South Korea]
6(4)	Thorn areoles present (Fig. 10.3 D)	7
6′	Thorn areoles absent	*Chordodes anthophorus* Kirjanova, 1950 [Georgia, Tajikistan, Uzbekistan]
	Or:	*Chordodes japonensis* Inoue, 1952 [Japan, South Korea]
7(6)	Bulging areoles present	8
7′	Bulging areoles absent	*Chordodes parabipilus* Kintsurashvili, Schmidt-Rhaesa & Gorgadze, 2011 [Georgia]
8(7)	Two types of crown areoles: one with long (Fig. 10.3 D) and one with short apical filaments	*Chordodes koreensis* Baek, 1993 [South Korea]
8′	Crown areoles with one type of apical filaments	*Chordodes moutoni* Camerano, 1895 [China: Ngan Haei]

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Phylum Mollusca

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Introduction to the Phylum

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INTRODUCTION

Two classes of molluscs occur in Palaearctic freshwater habitats: Gastropoda and Bivalvia. Molluscs are present in most Palaearctic freshwater habitats. Frequently terrestrial snails fall into aquatic habitats, and care should be taken not to confuse them with aquatic taxa. Many taxa are protected by local and regional conservation and/or fishing laws, and several invasive species have been reported in Palaearctic waters.

LIMITATIONS

Freshwater mollusc identification is primarily based on shell morphology. However, shell shape can be modified substantially by water currents, available minerals, and predatory pressures (summarized in Rogers & Wethington, 2007). Consequently, we recommend that identifications be based on a series of specimens when possible.

MATERIAL PREPARATION AND PRESERVATION

Empty shells should be gently cleaned using ethyl alcohol and water. Shells can be air dried. Whole animals and soft-tissue samples should be preserved according to the recommendations described below for each class.

KEYS TO MOLLUSCA

Mollusca: Classes

1	Single shell present which is coiled (snails) or uncoiled (freshwater "limpets")	**Gastropoda [p. 323]**
1′	Two equal shells (valves) present and connected by a ligament hinge; mussels and clams	**Bivalvia [p. 348]**

REFERENCE

Rogers, D.C. & A. R. Wethington. 2007. *Physa natricina* Taylor, 1988, junior synonym of *Physa acuta* Draparnaud, 1805 (Pulmonata: Physidae). Zootaxa 1662: 45−51.

Class Gastropoda

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INTRODUCTION

Snails and slugs (Gastropoda) constitute the most diversified class of Mollusca, with global species richness estimated as exceeding 60,000 species. This is the only class of molluscs that has conquered all three main domains of life in marine, freshwater, and terrestrial habitats. Overall gastropod diversity in continental waterbodies (fresh- and brackish waters) is not very high compared to their diversity in marine and terrestrial habitats. The most recent (and rather conservative) survey estimates place gastropod global richness in freshwater as 4,000 species (Strong et al., 2008). Gastropods are almost cosmopolitan in distribution, represented in freshwaters on all continents, excluding Antarctica (Starobogatov, 1970; Banarescu, 1990; Strong et al., 2008; Lydeard & Cummings, 2017). The Palaearctic maintains the most diverse continental aquatic snail fauna,

with upwards of 1,700 described species (Strong et al., 2008). Many freshwater gastropods are of great practical significance due to their role as helminthic disease vectors (fascioliosis, schistosomatosis, opisthorchosis, and many others, less injurious) and are an important component of freshwater food webs. Some freshwater snail species are notorious as effective and sometimes harmful invaders (for example, the apple snail species that became widely distributed in the tropics and subtropics as the result of the aquarium trade). Many species are threatened due to habitat loss and/or alteration (Cuttelod et al., 2011).

LIMITATIONS

The identification keys given in this chapter are far from complete. They encompass the gastropod families and genera living in Palaearctic continental waters, but only a small portion of species could be included. Many Palaearctic freshwater snails (for example, numerous Hydrobiidae) are so tiny and conchologically similar that one may identify them correctly only after thorough investigation of their internal anatomy and/or genetics.

The superfamily Hydrobioidea, with its more than 1,000 species (worldwide), is the most diverse Palaearctic freshwater gastropod group (Strong et al., 2008). This unparalleled diversity may be explained by repeated nonadaptive radiations (Wilke et al., 2010) that occurred in different regions of Europe, the Near East, and (to a lesser extent) central Asia. These snails are minute (typically up to 4 mm, rarely larger) and are common inhabitants of caves, springs, and wells, although some groups (Pyrgulinae) have radiated extensively in large lakes such as Ohrid, Prespa, and the Caspian Sea.

The volume and taxonomic structure of the Hydrobioidea have been hotly debated over the last several decades. Some authors accept it as a large family containing several morphologically divergent subfamilies (see, for example, Zhadin, 1952; Falkner et al., 2001; Glöer (2002)). Others have split this large group into a series of families (Radoman, 1983; Starobogatov & Sitnikova, 1983; Anistratenko & Stadnichenko, 1994; Bouchet & Rocroi, 2005). Here the second approach is followed, with Amnicolidae, Bythinellidae, Emmericiidae, Lithoglyphidae, and Tateidae considered separate families. Several subfamilies are also recognized.

As it would be impossible to present here even remotely complete keys to all hydrobiioid genera, let alone species, the keys are greatly restricted. Numerous small endemic hydrobiioid genera have been recently described (Arconada & Ramos, 2003; Glöer & Pešić, 2012; Boeters et al., 2013; Delicado et al., 2016), and that number will surely increase in the near future. Further insights into the diversity, taxonomy, and distribution of Palaearctic hydrobiioid snails can be found in Radoman (1983, 1985), Kabat & Hershler (1993), Bodon et al. (2001), Wilke et al. (2001), Glöer (2002), Arconada & Ramos (2003), Szarowska (2006), and Georgiev (2014). This list of references is far from complete. The south European and Caucasian hydrobiioid faunas are still not fully described, and discovery of many new species and genera is expected.

Furthermore, the level of taxonomic resolution concerning many gastropod taxa in portions of Asia where the Palaearctic and Oriental bioregions meet is still muddled and the keys are of more limited usefulness in these areas. Much of Afghanistan, China, Iran, Iraq, Korea, and Japan need additional surveys and focused taxonomic revisions of their gastropod fauna. Thus, we caution users of these keys when identifying material from those regions, especially regarding the lymnaeids, planorbids, semisulcospirids, and viviparids.

More information about the taxonomy, phylogeny, morphology, distribution and ecology of the Palaearctic freshwater Gastropoda can be obtained from the following: [general accounts] Cox (1960); Taylor (1988); Fretter & Graham (1994); Ponder & Lindberg (1997); Bouchet & Rocroi (2005); Sturm et al. (2006); Aktipis et al. (2008); [taxonomy and distribution] Starobogatov (1970); Banarescu (1990); Falkner et al. (2001); Glöer (2002); Welter-Schultes (2012); [ecology and conservation] Frömming (1956); Beriozkina & Starobogatov (1988); Økland (1990); Dillon (2000); Cuttelod et al. (2011); [regional surveys and keys] Germain (1931); Kozhov (1936); Zhadin (1952); Adam (1960); Piechocki (1979); van Damme (1984); Grossu (1986, 1987); Falniowski (1989); Økland (1990); Anistratenko & Stadnichenko (1994); Gittenberger et al. (1998); Glaubrecht (1993); Kerney (1999); Anistratenko & Anistratenko (2001); Starobogatov et al. (2004); Kantor et al. (2010); Welter-Schultes (2012); Horsák et al. (2013); Glöer (2015); Kiyashko et al. (2016); Piechocki & Wawrzyniak-Wydrowska (2016), Vinarski & Kantor (2016) (websites) MolluscaBase—http://www.molluscabase.org/, Fauna Europaea—http://www.faunaeur.org/, The IUCN Red List of Threatened Species—http://www.iucnredlist.org/.

TERMINOLOGY AND MORPHOLOGY

All Palaearctic freshwater snails have shells. The shell represents the external skeleton. The gastropod morphospace encompasses an enormous number of shell structure variants of size, proportions, and sculptural elements. Roughly, all the shell diversity can be distributed among four morphological types, whose differences and characteristic traits are depicted in Fig. 11.1 A. Further divisions within a particular type are also possible. For example, among turbospiral shells one may discern turriculate, auriculate, ovoid, ovate-conical, valvatoid, and other types (Fig. 11.1 B).

A snail shell may be dextral (or right-coiled) or sinistral (or left-coiled) (Fig. 11.1 C), and a particular coiling direction may characterize higher taxa of gastropods (families, subfamilies, sometimes genera within a family). Several main structural parts of the gastropod shell such as spire, aperture, body whorl, and operculum (in gill-breathing taxa), can be discerned (Fig. 11.1 D). Their absolute and relative sizes and proportions are significant for the purpose of exact taxonomic identification. However, it should be noted that many groups (the Lymnaeidae is a notorious example) exhibit extreme variability that may make their shell traits misleading for identification, and in such circumstances anatomical and molecular data give much more reliable information. Shells of dioecious freshwater snails (such as *Viviparus*) may exhibit some level of sexual dimorphism in size and proportions.

In addition, some other terms related to gastropod shell morphology are explained here (see full glossary in Cox, 1960):

Shell aperture: the opening in the shell through which the animal extends.

Shell axis: an imaginary line through the shell apex about which whorls are coiled (not applicable to limpets).

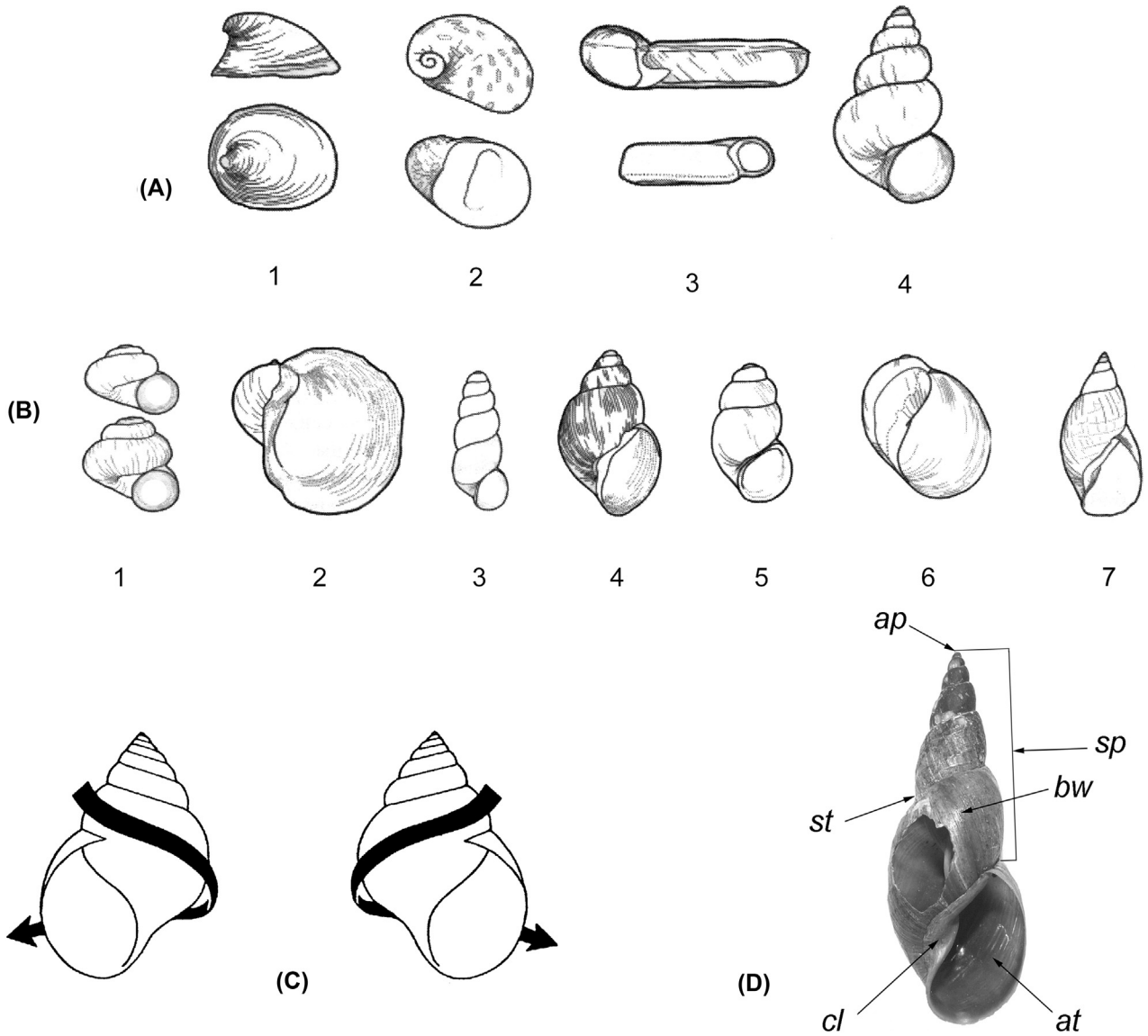


FIGURE 11.1 External morphology of gastropod shells: (A) four main structural types of gastropod shells: (1) patelliform (limpets), (2) neritiform (semiglobose), (3) planispiral, and (4) turbospiral; (B) main variants of turbospiral shells: (1) valvatoid (low conical), (2) auriculate (ear-shaped), (3) turriculate, (4) ovate-conical, (5) ovoid, (6) globose, and (7) high conical; (C) sinistral (left) and dextral (right) gastropod shells; (D) terminology of various parts of gastropod shell: *ap*, apex; *at*, aperture; *bw*, body whorl (last whorl); *cl*, columellar lip; *sp*, spire; *st*, suture. *(A and B) Shell pictures from Kiyashko et al. (2016); (C) after Burch (1989).*

Sculpture: a relief pattern on the shell surface. It may be represented by **ribs** or **riblets**, thin **striae**, small depressions, ridges, and other structures. Some gastropod shells virtually lack any prominent sculpture, being smooth and glossy. If sculptural elements are oriented parallel to the shell axis, then these are designated as **radial sculpture**. The **spiral sculpture** is formed by sculptural elements oriented transversely to axis.

Keel: a prominent spiral ridge of a shell. It may be solid or relatively soft, in the latter case the keel may look like a thin and fragile fringe on the shell edge.

Umbilicus: a cavity or depression formed around the shell axis inside the body whorl and situated at the base of the shell. The relative depth and width of the umbilicus may serve as a useful distinguishing character in some taxa of freshwater snails.

Operculum: this is comparable to a door, attached to the dorsum of the snail's foot that closes the shell aperture when the animal withdraws inside.

The absolute shell size is very plastic in most taxa and therefore is generally avoided in identification keys (though it may be useful for fast identification of some families or genera). There are many factors influencing shell size, including age (ontogenic variation), ambient temperature, food supply, parasitism, and so on. Shell proportions are thought to be a rather more reliable source of taxonomically relevant information. In order to use shell proportions for species identification, different **conchometric indices** are calculated on the basis of plain measurements. For example, one may use the ratio between shell width and shell height (SW/SH; see measurements schemes below) for characterization of relative slenderness of a snail shell, and so on. These ratios, however, are also prone to change with age, which is explained by the allometric growth.

All the keys given in this chapter are based on traits of adult (definitive) animals and do not take into account possible ontogenic changes in size and proportions of shells and reproductive structures. For the sake of uniformity, shells of all gastropod families, except Physidae, are regarded in the keys below as dextral, with aperture situated rightwards from the shell axis (though it may not be true for some representatives of planispiral Planorbidae).

The soft body (Figs. 11.2 A, B) is divided into three major parts—head, foot, and visceral sac (=visceral hump). The latter portion is usually hidden within the shell. Among the internal organs, those of the reproductive system are most often used in identification, especially in pulmonate snails (Heterobranchia: Lymnaeiformes). It is assumed that the genitals are insulated from the direct influence of environmental factors and thus genital traits are more stable than those of the shells.

Inside the mouth is the **radula**, a tongue-like organ that bears rows of teeth. The radula is used to rasp food from various surfaces and draw it inside the mouth. The radular structures (number and position of teeth of different kind) are generally considered as less significant for systematics and identification, especially at lower levels (subgenus, species).

Roughly, all freshwater snails may be divided into two anatomically different groups. The first is the branchiate gastropods, which is constituted by representatives of the subclasses Neritomorpha, Caenogastropoda, and the family Valvatidae. All snails of this group use gills (or a single gill) for breathing. The presence of an operculum is another diagnostic trait of this group. The pulmonate snails (Lymnaeiformes or Hygrophyla) form the second set of taxa. These animals typically use atmospheric air for their breathing and have a special respiratory organ, the lung. The operculum is absent in all Pulmonata.

The most taxonomically significant structures of the Pulmonata reproductive system are presented in Figs. 11.2 C, D. For an exact discrimination among species and genera in some families (especially Lymnaeidae) the ratio between the lengths of the two structural parts of the copulatory organ (i.e., **praeputium** and **penis sheath;** see Fig. 11.2 C) is used. Though this ratio (sometimes designated as ICA = index of the copulatory apparatus) is somewhat variable within populations and may change with age (Beriozkina & Starobogatov, 1988), its use is sometimes more effective than the examination of shells. In some lymnaeid taxa (i.e., *Stagnicola*) it is almost impossible to determine the species without dissection and calculation of ICA. In Planorbidae, some closely related and conchologically similar species may be distinguished only after calculation of the number of their prostate diverticulae (Fig. 11.2 D).

The relative length and proportions (long and narrow vs. short and thick) of the **spermathecal duct** as well as determination of the number of internal prostate folds (Fig. 11.2 D) are useful for discrimination among genera and subgenera of Lymnaeidae.

Other, much more minute anatomical traits (such as size, shape, and position of the **penis stylet** in some Planorbids), are used, but their examination requires a lot of subtle and thorough dissections, and hence they are not considered here.

Measurement Schemes

A measurement scheme has been developed for each gastropod shell structural type (Fig. 11.1). However, the schemes proposed by different authors may differ in some details from each other even in application to the same structural type. Figs. 11.3 A–C represents measurement schemes of **turbospiral, planispiral**, and **patelliform** shell adopted here.

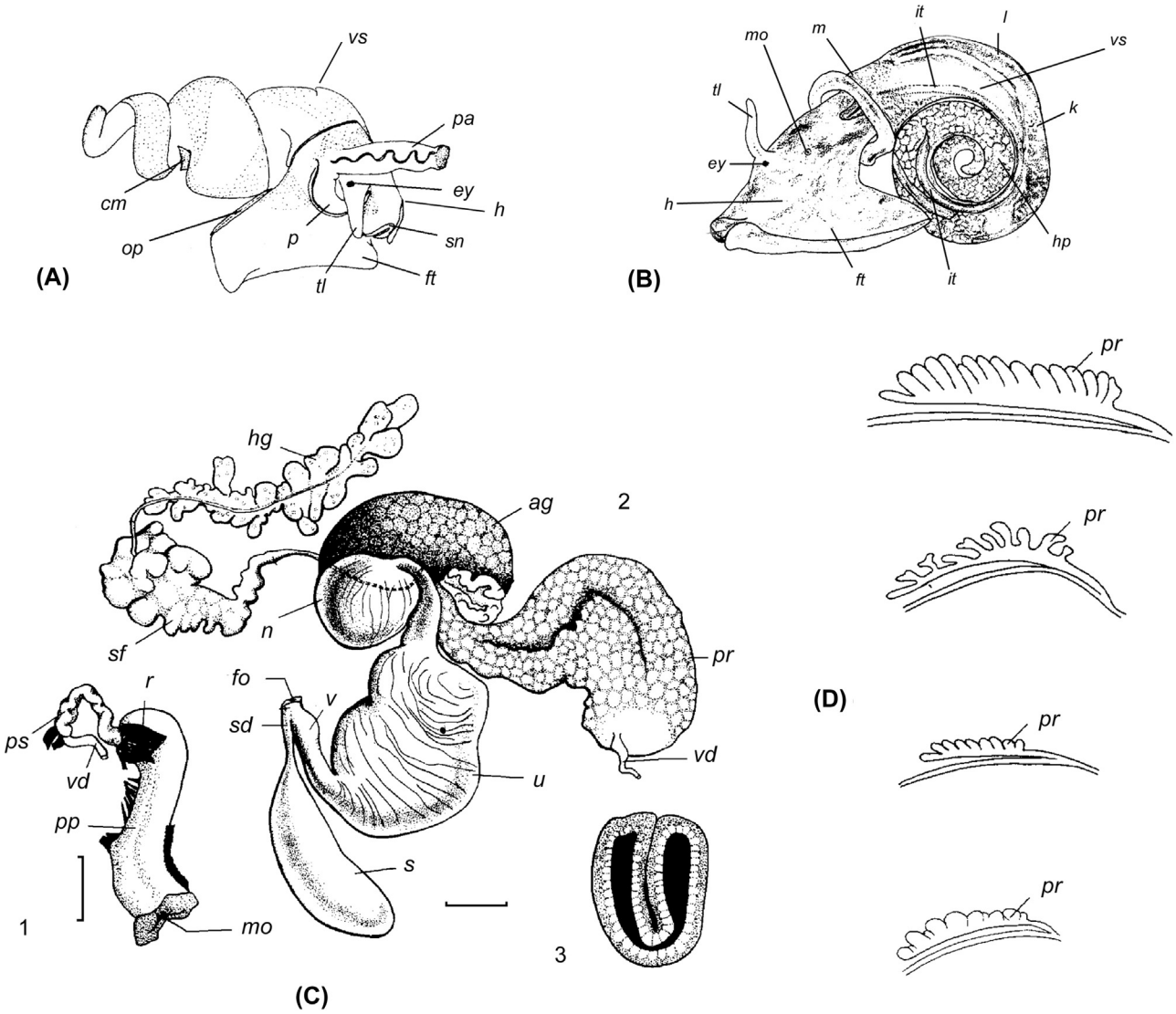


FIGURE 11.2 External and internal structure of freshwater snails (fragments): (A) external soft body morphology of a branchiate freshwater gastropod (*Bythinella*); (B) external soft body morphology of a pulmonate freshwater gastropod (*Gyraulus*); (C) reproductive system of lymnaeid snails: (1) copulatory apparatus, (2) female genital tract and the hermaphroditic part of the reproductive system, (3) internal section of the prostate where a single internal fold is seen; (D) variants of the prostate structure in some planorbid snails. Scale bars, 1 mm. *ag*, albumen gland; *cm*, columellar muscle; *ey*, eye; *fo*, female genital opening; *ft*, foot; *h*, head; *hg*, hermaphroditic gland; *it*, intestinal tract; *m*, mantle; *mo*, male genital opening; *n*, nidamental gland; *op*, operculum; *p*, penis; *pa*, penis appendix; *pp*, praeputium; *pr*, prostate; *ps*, penis sheath; *r*, praeputium retractor; *s*, spermatheca; *sd*, spermathecal duct; *sf*, seminal follicles; *sn*, snout; *tl*, tentacle; *u*, uterus; *v*, vagina; *vd*, vas deferens; *vs*, visceral sac. *(A) After Jungbluth (1971), modified; (B) after Meier-Brook (1983); (C) after Beriozkina & Starobogatov (1988), slightly simplified; (D) after Glöer (2002).*

Many genera and subgenera differ from each other by the maximum number of shell whorls. The method for counting whorls is presented in Fig. 11.3 D.

The shell **tangent-line** is an imaginary line that "just touches" the surface of all or several of the whorls constituting the spire. It may be straight or almost straight, convex or concave (Fig. 11.3 E). The form of this line may be species-specific and in certain cases allows one to distinguish between closely allied and conchologically similar species.

MATERIAL PREPARATION AND PRESERVATION

Whole animals can be preserved in ethyl or isopropyl alcohol. Formalin should never be used, as it will dissolve the shells and obstructs soft body dissections. Empty shells can be kept dry. A bit of cotton stuffed carefully in the aperture and daubed with glue will hold the operculum in place. Shells that have had the animal removed should be

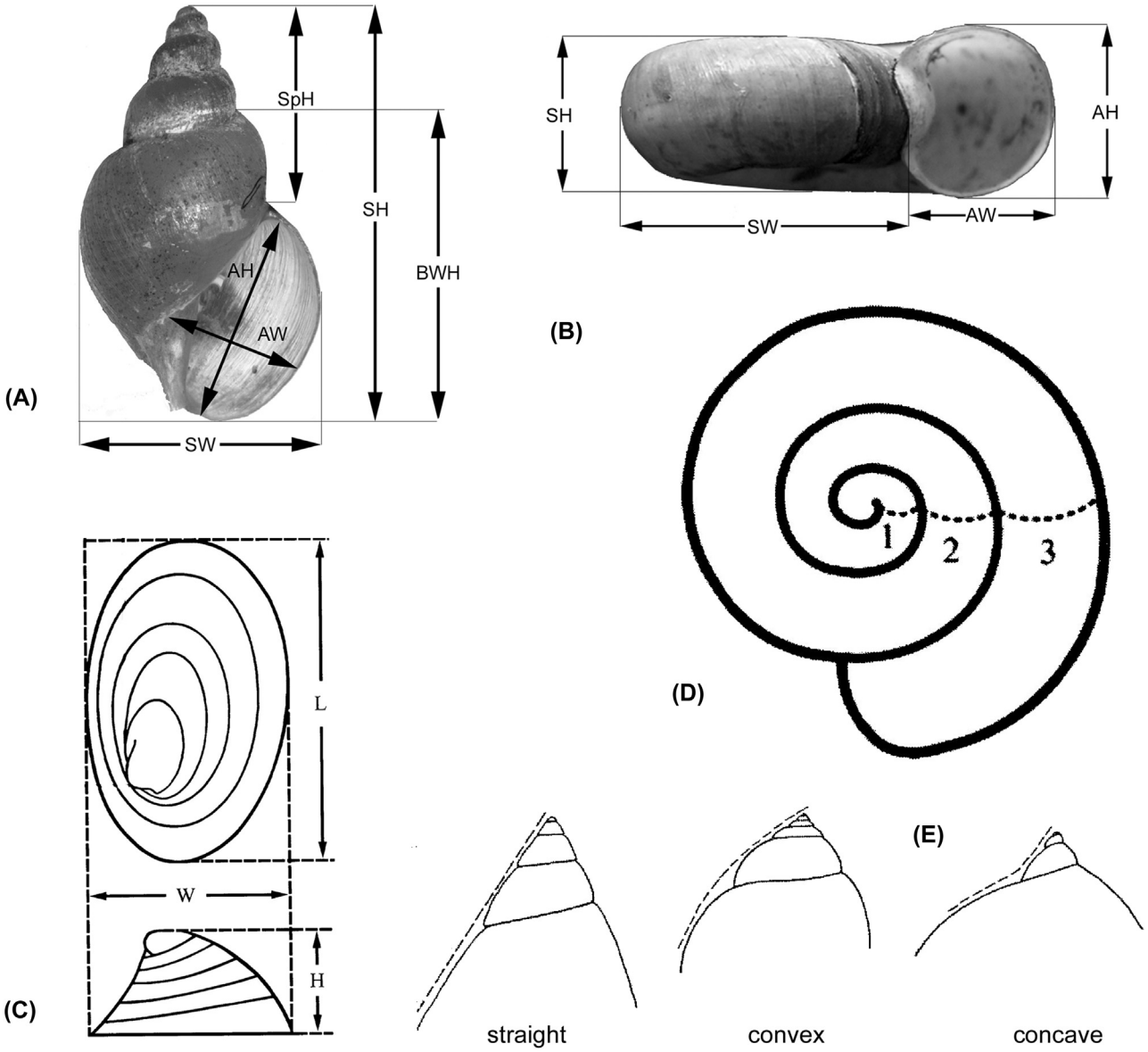


FIGURE 11.3 Schemes of measurements of turbospiral (A), planispiral (B), and patelliform (C) shell, whorls counting (D), and the tangent-lines of different shells (E). *AH*, aperture height; *AW*, aperture width; *BWH*, body whorl height; *H*, shell height (in patelliform shell); *L*, aperture length; *SH*, shell height; *SpH*, spire height; *SW*, shell width; *W*, aperture width (in patelliform shell). *(A and B) Original; (C) after Shirokaya et al. (2012), greatly simplified; (D) after Burch (1989); (E) after Kruglov (2005).*

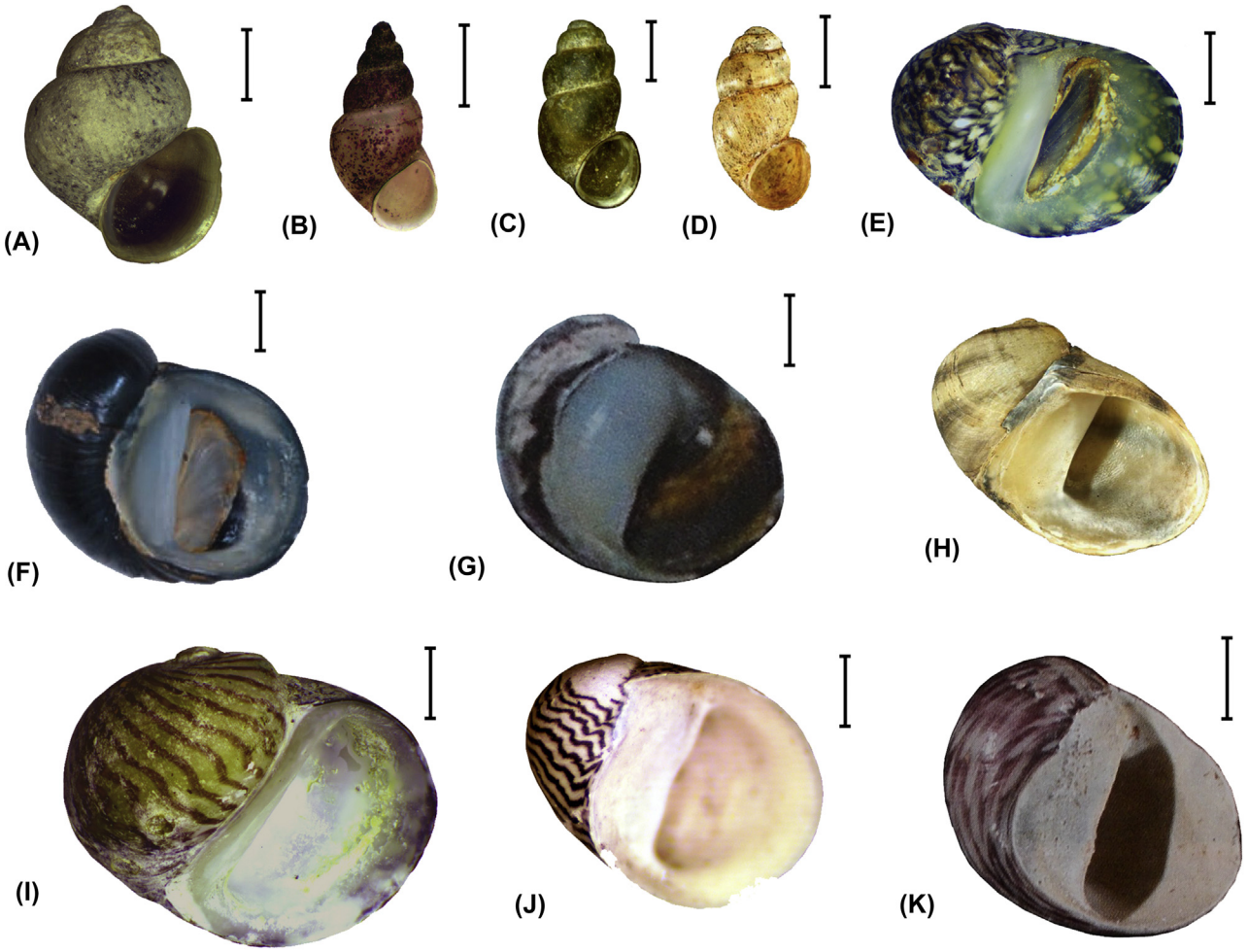


FIGURE 11.4 (A) *Emmericia ventrosa*; (B) *Potamopyrgus antipodarum*; (C) *Bythinella austriaca*; (D) *B. luteola*; (E) *Theodoxus fluviatilis*; (F) *T. prevostianus*; (G) *T. baeticus*; (H) *T. transversalis*; (I) *T. danubialis*; (J) *T. pallasi*; and (K) *T. meridionalis*. Scale bars: 1 mm (C and D), 2 mm (A, B, E–G, and I–K), absent in the original source (H). *All photos are original, except D (after Glöer & Pešić, 2010b), F (after Fehér et al., 2009), H (after Glöer & Pešić, 2015), G and K (after Welter-Schultes, 2012, modified).*

cleaned with alcohol inside and air allowed to dry them to reduce odors.

Specimens where the animal needs to be extracted from the shell can be boiled in pure bleach for a few seconds or dipped in concentrated hydrochloric acid for a few seconds. Alternatively, the shell can be gently cracked with forceps and the shell pieces removed. The radula can be viewed by cutting open the top of the head and teasing the structure out with a needle, probe, or forceps.

The genitalia sit inside the headfoot just above and behind the eyes. Using a fine scalpel or a razor, gently cut the head open posteriorly between the eyes. The genitalic penile structures lie on either the right or the left side of the animal, behind and at the base of the tentacle.

ACKNOWLEDGMENTS

Maxim Vinarski's work on Palaearctic snail taxonomy has been supported financially by the Russian Ministry for Higher Education and Science (project No. 6.1352.2017/4.6) and the President of the Russia Grant Council (project No. MD-2394.2017.4).

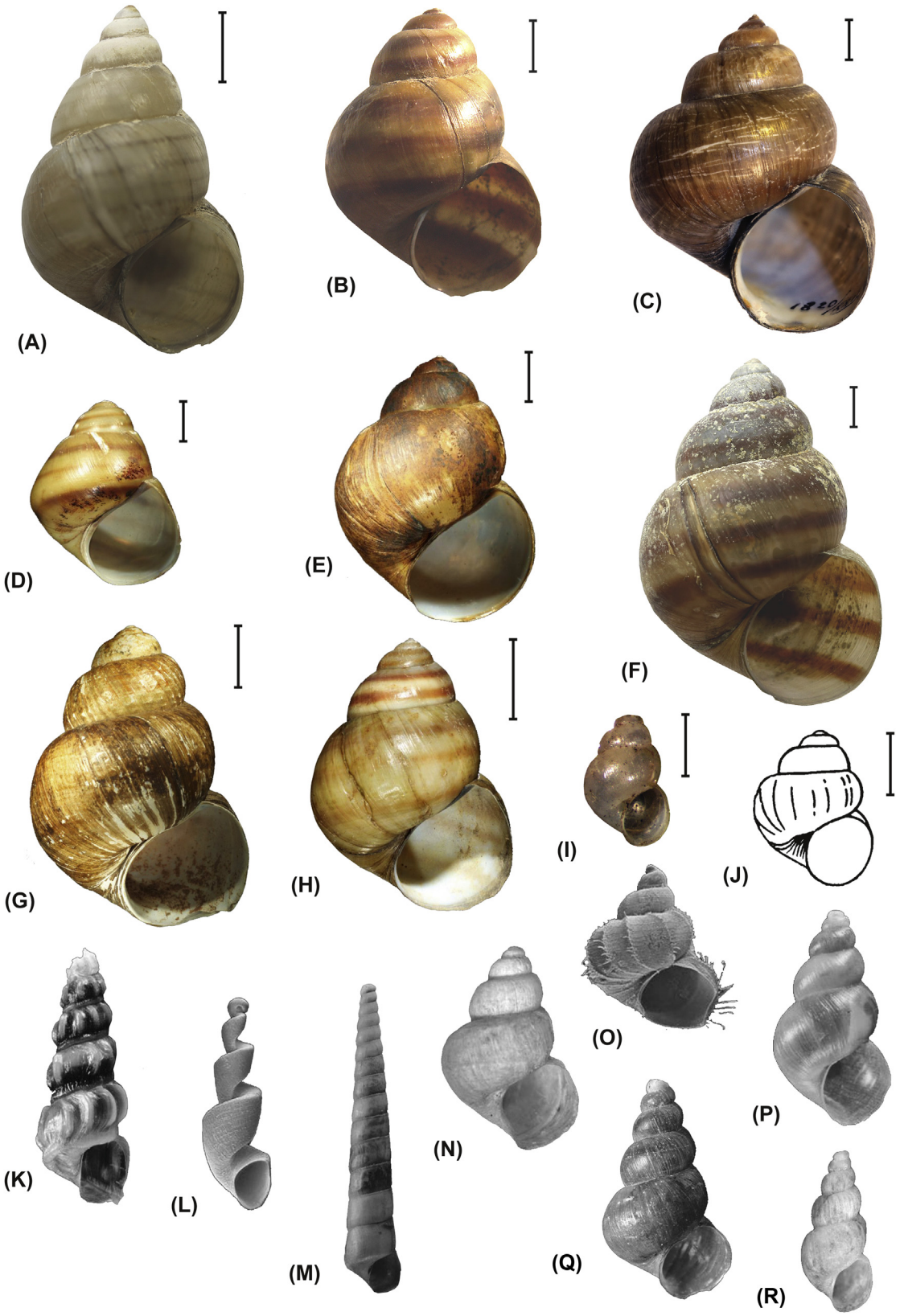


FIGURE 11.5 (A) *Bellamya bengalensis*; (B) *Viviparus viviparous*; (C) *V. contectus*; (D) *V. hellenicus*; (E) *V. sphaeridus*; (F) *V. ater*; (G) *V. mamillatus*; (H) *V. acerosus*; (I) *Marstoniopsis steinii*; (J) *Kolhymamnicola kolhymensis*; (K) *Baicalia dybowskiana*; (L) *Liobaicalia stiedae*; (M) *Godlewskia godlewskii*; (N) *Maackia bythiniopsis*; (O) *Teratobaikalia ciliata*; (P) *Korotnevia semenkewitchi*; (Q) *Parabaikalia florii*; and (R) *Pseudobaikalia zachwatkini.* Scale bars: 1 mm (I and J), 5 mm (A–H), (K–R) scale bars absent in the original source. *(A–C, F, and I) Original photos; (D, E, G, and H) after Glöer & Georgiev (2014); (J) after Starobogatov & Streletzkaja (1967); (K–R) after Sitnikova (2012), slightly modified.*

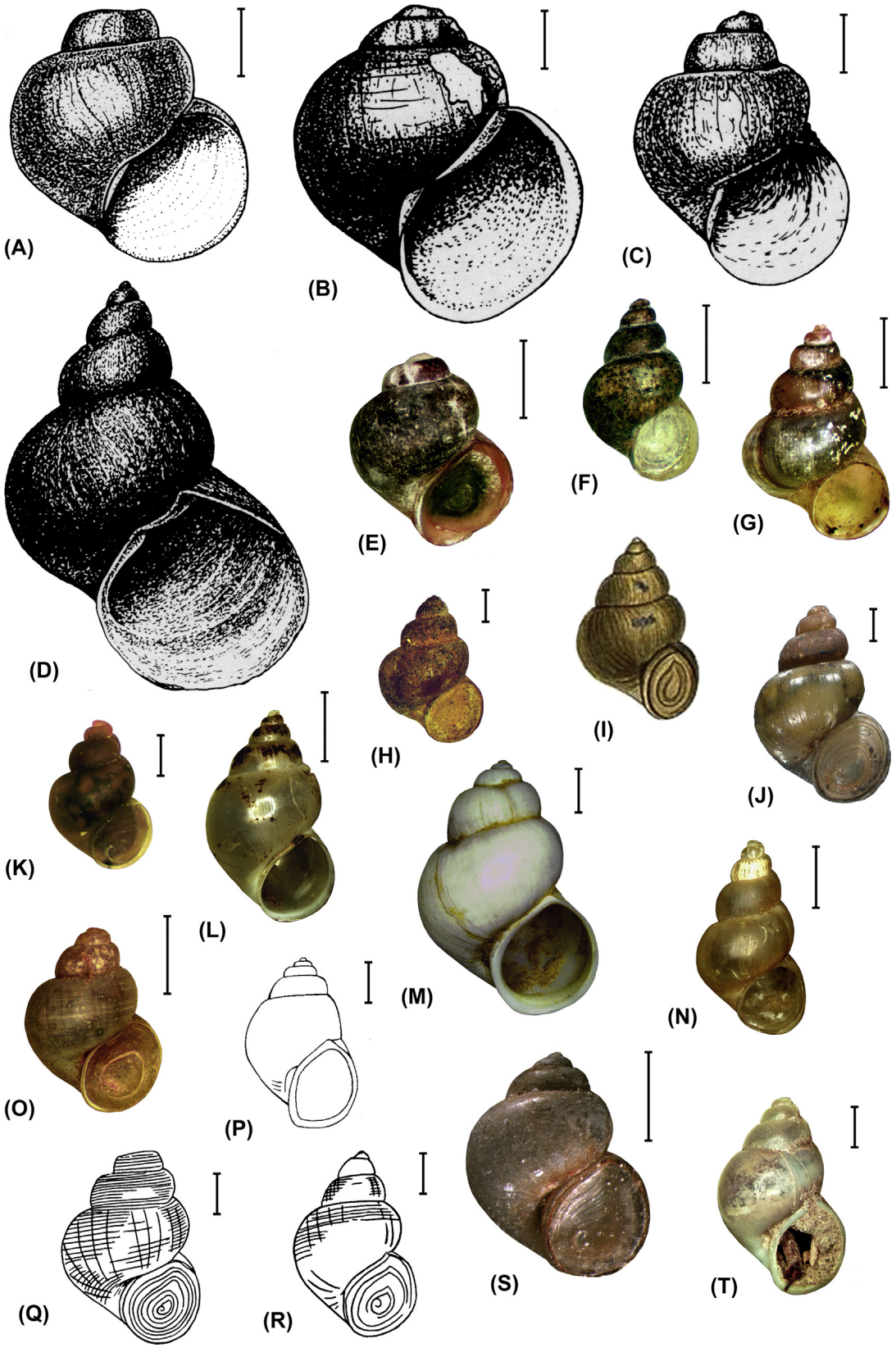


FIGURE 11.6 (A) *Kobeltocochlea* (*Pseudobaikalia*) *michnoi*; (B) *Kobeltocochlea* (*Kobeltocochlea*) *olchonensis*; (C) *Benedictia* (*Baicalocochlea*) *baicalensis*; (D) *Benedictia* (*Benedictia*) *fragilis*; (E) *Pseudobithynia irana*; (F) *Pseudobithynia westerlundi*; (G) *Bithynia troschelii*; (H) *B. leachii*; (I) *B. boissieri*; (J) *B. kastorias*; (K) *B. prespensis*; (L) *B. tentaculata*; (M) *B. mostarensis*; (N) *B. zeta*; (O) *B. hellenica*; (P) *Digoniostoma kashmirensis*; (Q) *Boreoelona sibirica*; (R) *Boreoelona contortrix*; (S) *Alocinma caspia*; and (T) *Alocinma sistanica*. Scale bars: 1 mm (H, J, and K), 2 mm (A–C, E–G, and L–T), absent in the original source (D and I). *All pictures are original, except A–D (after Sitnikova, 1995), I (after Küster, 1852), P (after Izzatullaev, 1982), R and S (after Starobogatov & Streletzkaja, 1967), T (photo, I. Nekhaev).*

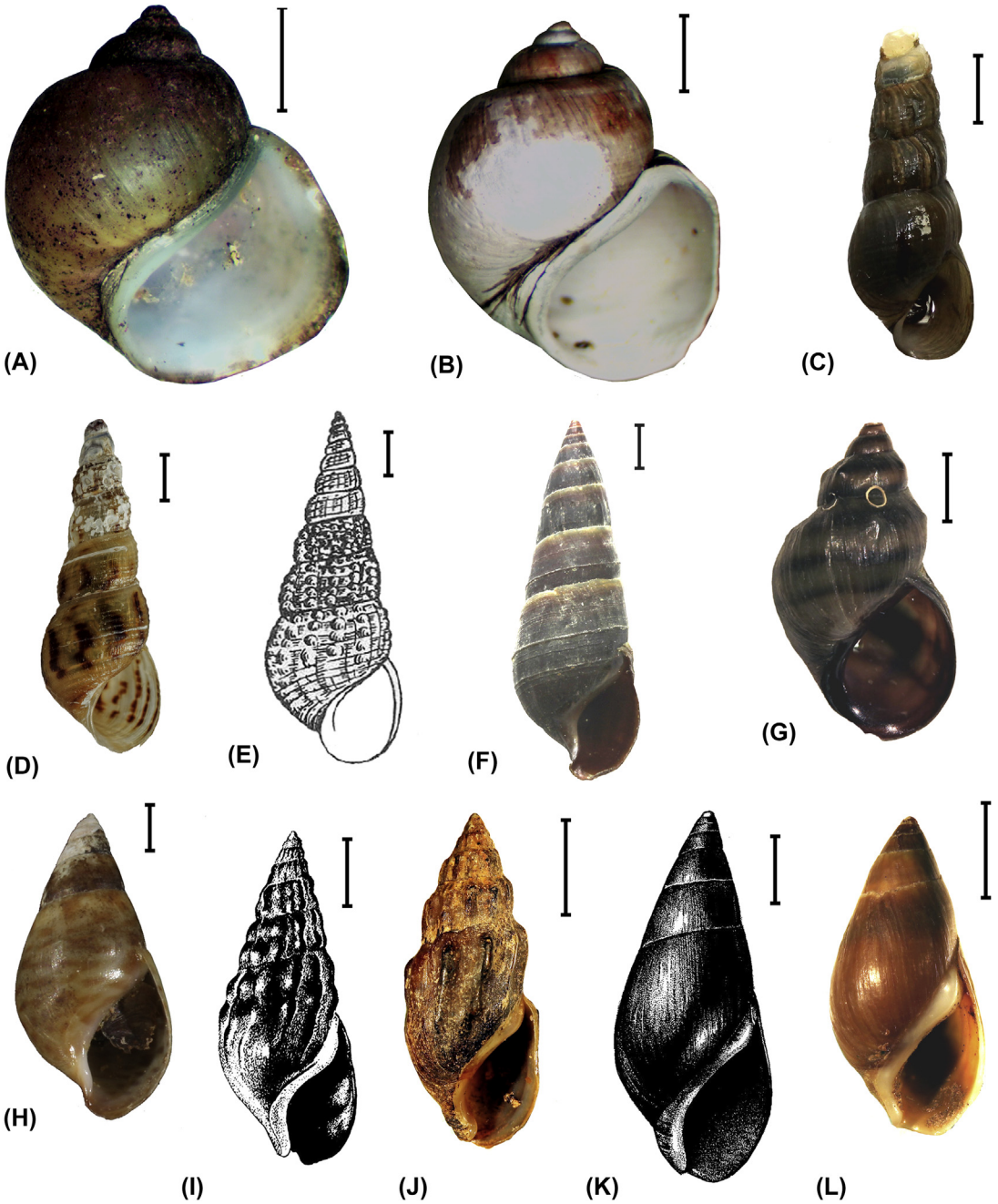


FIGURE 11.7 (A) *Lithoglyphus naticoides*; (B) *L. pyramidatus*; (C) *Melanoides tuberculata*; (D) *M. pamiricus*; (E) *M. kainarensis*; (F) *Microcolpia daudebartii*; (G) *Holandriana holandrii*; (H) *Esperiana esperi*; (I) *Melanopsis saulcyi*; (J) *Melanopsis costata*; (K) *Melanopsis buccinoidea*; and (L) *Melanopsis praemorsa*. Scale bars: 2 mm (except I–L—5 mm). *All pictures are original, except, D (photo, D. Palatov), E (after Starobogatov & Izzatullaev, 1980), H (after Welter-Schultes, 2012), I, K (after Heller et al., 2005).*

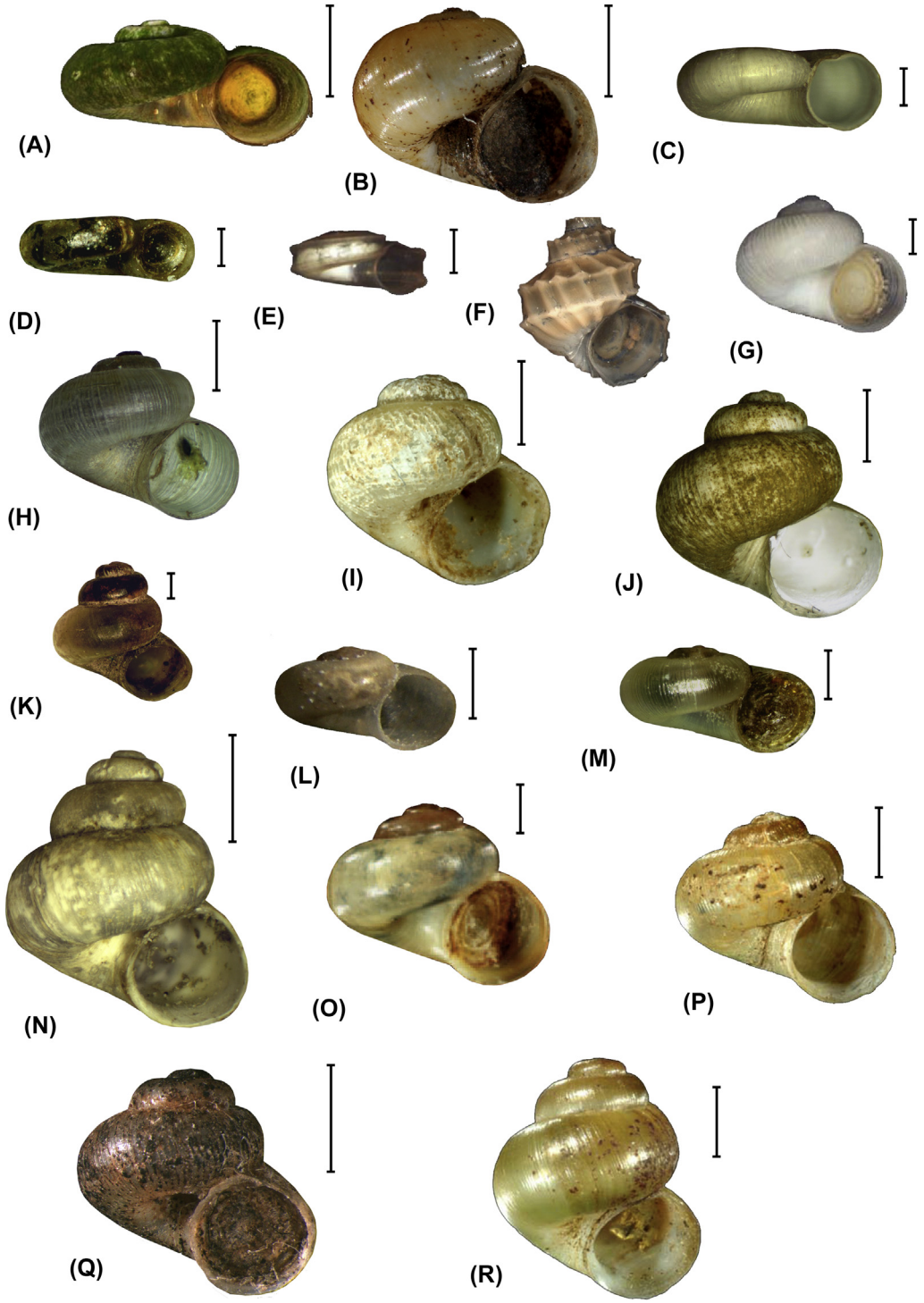


FIGURE 11.8 (A) *Megalovalvata baicalensis*; (B) *Borysthenia naticina*; (C) *Valvata sibirica*; (D) *V. cristata*; (E) *V. relicta*; (F) *V. klemmi*; (G) *V. rhabdota*; (H) *V. brevicula*. (I) *V. aliena*. (J) *V. confusa*. (K) *V. geyeri*. (L) *V. saulcyi*; (M) *V. macrostoma*; (N) *V. antiqua*; (O) *V. studeri*; (P) *V. ambiqua*; (Q) *V. discors*; and (R) *V. piscinalis*). Scale bars: 1 mm (A, C–E, G, and K–M), 2 mm (B, H–J, and N–R), absent in the original source (F). *All photos are original, except A (after Sitnikova, 2012), B and L (after Welter-Schultes, 2012), E and G (after Hauswald et al. 2008), F (photo, K. Schreiber; www.arkive.org), I (photo, P. Glöer), O, P, and S (after Vinarski et al., 2013a).*

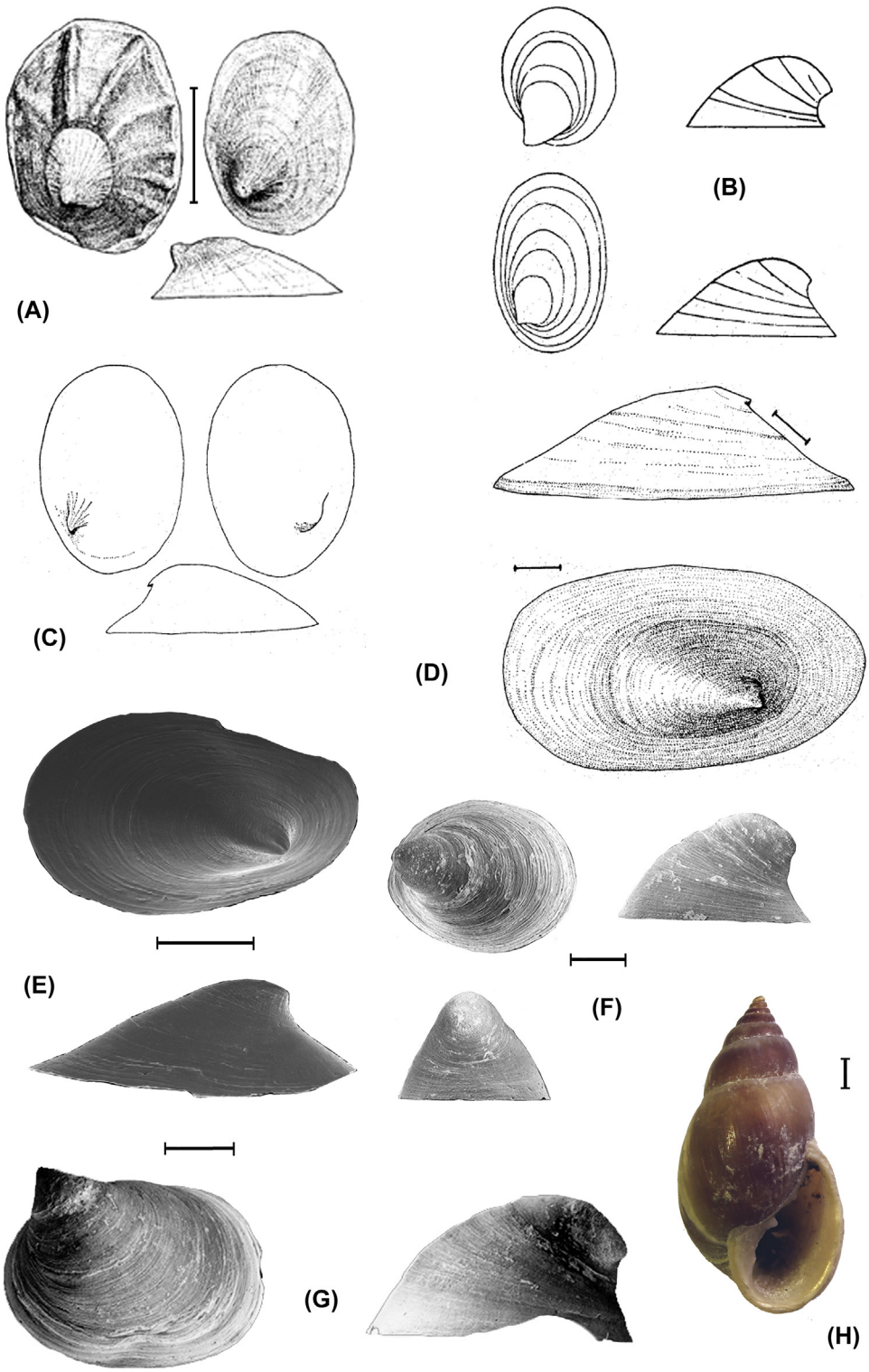


FIGURE 11.9 (A) *Acroloxus macedonicus*; (B) *A. tetensi*; (C) *A. improvises*; (D) *A. lacustris*; (E) *A. baicalensis*; (F) *Gerstfeldtiancylus benedictiae*; (G) *Pseudancylastrum sibiricum*; and (H) *Myosotella myosotis.* Scale bars 1 mm (B and C—scale bars absent in the original source). *(A–D) After Hubendick (1972); (E) after Shirokaya et al. (2011); (F and G) after Shirokaya et al. (2003).*

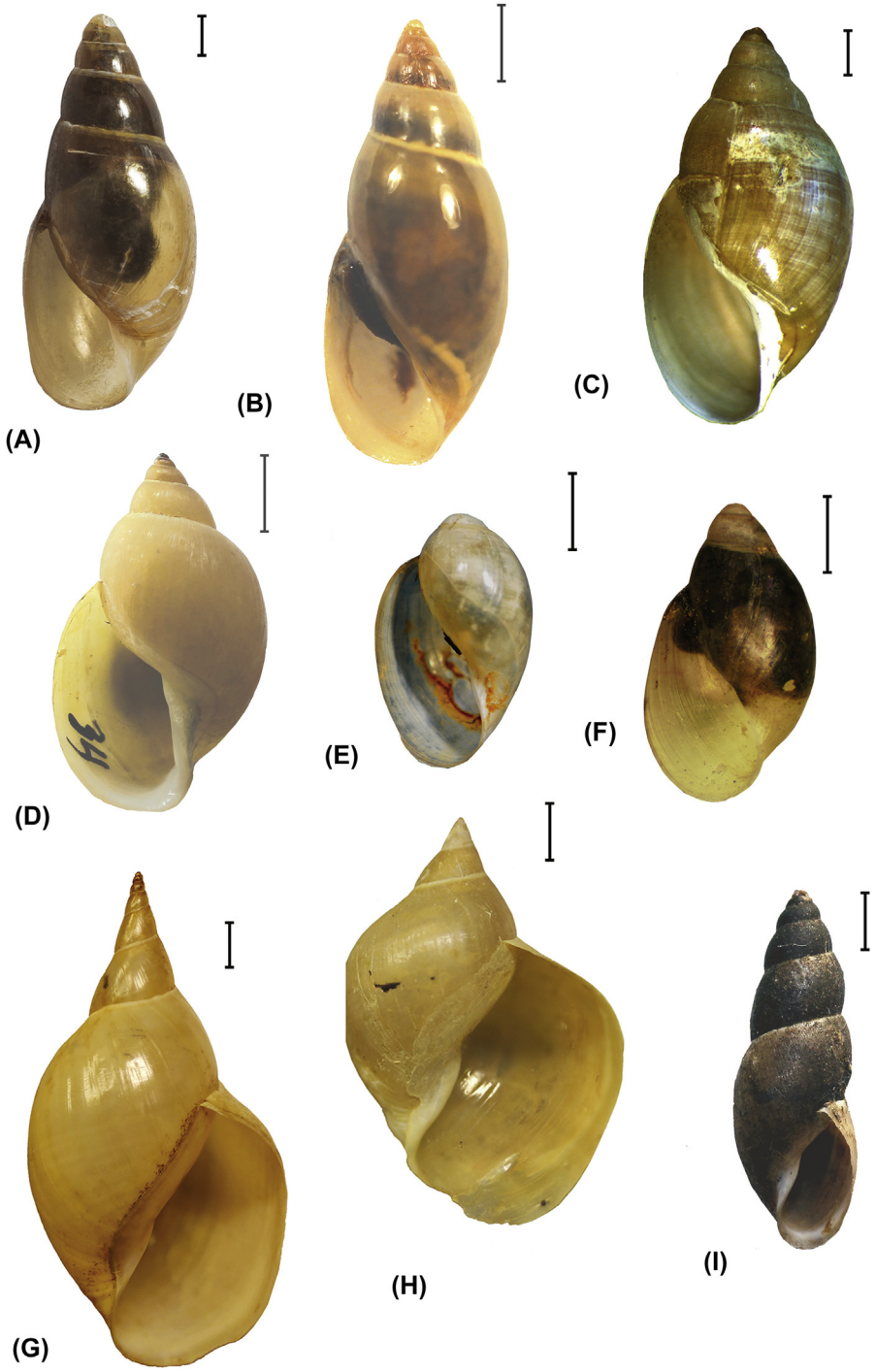


FIGURE 11.10 (A) *Aplexa hypnorum*; (B) *Sibirenauta elongata*; (C) *Sibirenauta sibirica*; (D) *Physa acuta*; (E) *P. fontinalis*; (F) *P. taslei;* (G) *Lymnaea stagnalis*, the typical morphotype; (H) *L. stagnalis*, the ear-shaped morphotype; and (I) *Omphiscola glabra*. Scale bars 1 mm (A and C), 2 mm (B, D–F, and I), 5 mm (G and H). *All photos are original, except C (after Vinarski et al., 2015).*

KEYS TO GASTROPODA

These keys are based partially on keys provided by Radoman (1983), Anistratenko & Stadnichenko (1994), Glöer (2002), Starobogatov et al. (2004), Sitnikova (2012), and Kiyashko et al. (2016). The taxonomic framework used here follows, with minor exceptions, the system accepted by WoRMS team (http://www.marinespecies.org/aphia.php?p=taxdetails&id=101).

Gastropoda: Subclasses

1	Shell operculate	2
1′	Operculum absent	Heterobranchia, one order: **Lymnaeiformes** (=Hygrophyla)
2	Shell turbospiral or planispiral	3
2′	Shell neritiform	Neritimorpha, one family: **Neritidae [p. 337]**
3	Shell smaller, definitive size 20 mm or less, if larger then body whorl without dark bands	4
3′	Shell relatively large, definitive size not less than 25 mm (up to 30–35 mm), usually with several dark bands on body whorl	Caenogastopoda (In part)
4	Shell valvatoid (Fig. 11.1 B) or planispiral, with perfectly round or rounded aperture; shell height less 10 mm	5
4′	Shell of other shape, if aperture rounded then shell height exceeds 10 mm	**Caenogastopoda** (in part)
5	Shell width ≥3 mm; found in lakes, ponds, and slowly running rivers and streams	Heterobranchia, one family; **Valvatidae [p. 342]**
5′	Shell width less than 2.2 mm. In subterranean waters, springs, and other minor and shallow waterbodies	**Caenogastopoda** (in part)

Gastropoda: Heterobranchia: Lymnaeiformes: Superfamilies

We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell not patelliform, or if patelliform, then spire sinistral (apex centered or to right of midline) and blunt, with adult patelliform shell larger than 7 mm (Figs. 11.12 A, B, D–G)	2
1′	Shell patelliform with spire dextral (apex to left of midline), acute; adult shell less than 7 mm in length (Figs. 11.9 A–C). [*Acroloxus* is widespread in the Palaearctic but three endemic genera occur in the Lake Baikal Basin, see Figs. 11.9 E–G]	Acroloxoidea, one family; Acroloxidae
2(1)	Tentacles narrow, filiform	3
2′	Tentacles, broad, flat, triangular; hemoglobin absent; coiled shell always dextral (plates 7–9)	Lymnaeoidea, one family: **Lymnaeidae [p. 323]**
3(2)	Aperture with three teeth on columella only (Fig. 11.9 H); shell elongate; hemoglobin absent from blood; estuaries ... [Coastal Europe]	Ellobioidea, one family: Ellobiidae: *Myosotella myosotis* (Draparnaud, 1801)
3′	Aperture without teeth, or with teeth set back, inside aperture, never on columella; shell elongate, patelliform, planospiral, fusiform, or succiniform; if patelliform, then shell apex central or sinistral; coiled shell dextral or sinistral (Figs. 11.7 and 11); hemoglobin present in blood or not	**Planorboidea [p. 326]**

Gastropoda: Heterobranchia: Lymnaeiformes: Lymnaeidae: Genera and Subgenera

A large and diverse family distributed on all continents except Antarctica (Hubendick, 1951; Starobogatov, 1970; Banarescu, 1990). The highest species richness is in North America and Eurasia, especially in temperate latitudes. The Palaearctic region has not less than 30 (some researchers accept much more valid species, up to 150–200; see Kruglov, 2005) species, in two subfamilies and 10–12 genera and subgenera (Vinarski, 2013). Due to high levels of intra- and interspecific variation in shell shape and proportions and numerous instances of parallel evolution in conchological traits of the lymnaeids, their identification is not always possible by shells alone. We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell not exceeding 35 mm, usually much smaller	2
1′	Shell large as much as 40–65 mm (Figs. 11.10 G, H) [Holarctic]	*Lymnaea* (*Lymnaea* s. str.) *stagnalis* (L., 1758)
2(1)	Shell not as below, or if turriculate or cylindrical, animal has a single prostate fold	3

2′	Shell turriculate or almost cylindrical; prostate without internal folds (Fig. 11.10 I) ..... *Omphiscola glabra* (O.F. Müller, 1774) [Europe]
3(2)	Prostate with 2−10 internal folds 4
3′	Prostate with a single internal fold, or folds absent with shell very thin, fusiform, with spire acute and aperture ovate 5
4(3)	Whorls strongly convex (almost stepped); penis sheath wide, proximal part prominently tumid (Fig. 11.11 A) .... *Lymnaea* (*Kazakhlymnaea*) *taurica* (Clessin, 1880) [southeastern Europe eastward to southwestern Siberia]
4′	Whorls almost flat or weakly convex; penis sheath narrow, without a clear proximal tumidity ..... ***Stagnicola*** (in part)
5(3)	Penis sheath simple, not separated into parts 6
5′	Penis sheath consisting of two parts: muscular and glandular (Fig. 11.11 B) ..... *Aenigmomphiscola* Kruglov & Starobogatov, 1981 [Kazakhstan, Russia]
6(5)	Shell spheroid, ovoid, ovate-conical or auriculate, spire relatively short; shell width usually much greater than height 7
6′	Shell turriculate, turriculate-conical or high-conical, with spire relatively oblong, prominent; shell width is usually much less than height 10
7(6)	Mantle never covering shell externally; shell shape not as below 8
7′	Shell is covered outside by mantle; shell almost spheroid, very fragile, with spire almost invisible, sometimes involute (Fig. 11.11 C) ..... *Myxas glutinosa* (O.F. Müller, 1774) [western Palaearctic]
8(7)	Aperture columellar margin with depression weak or absent 9
8′	Aperture columellar margin with a strongly developed depression ..... ***Radix*** (in part) [Holarctic]
9(8)	Shell slender, fusiform, fragile, with spire more or less acute; prostate without internal folds (Fig. 11.12 A) .... *Pseudosuccinea columella* (Say, 1817) [widespread invasive. Nearctic]
9′	Shell form not as above, if fusiform, then spermathecal duct is very short or almost absent and prostate with a single internal fold .... ***Radix*** (in part)
10(6)	Shell small up to 15 mm, with stepped or convex whorls 11
10′	Shell up to 30 mm, if small, then whorls are flat or weakly convex (not stepped) 13
11(10)	Penis sheath relatively long and narrow 12
11′	Penis sheath short and strongly inflated (Figs. 11.11 K, L) ..... *Galba* (*Galba*) [widespread]
12(11)	Whorls strongly convex (stepped), ovate-conical or ovoid with low spire ..... ***Orientogalba*** [central Asia]
12′	Whorls moderately convex (not stepped), shell turriculate-conical (Fig. 11.11 D) ..... *Galba* (*Sibirigalba*) *sibirica* (Westerlund, 1885) [Siberia, Mongolia, Far East]
13(10)	Columellar lip relatively thick, chalky white; praeputium dark, its width slightly greater than penis sheath width (Fig. 11.11 E) .... *Ladislavella* (*Ladislavella*) *terebra* (Westerlund, 1885) [Siberia, eastern Europe]
13′	Columellar lip not thick; praeputium usually light-colored, penis sheath much narrower than praeputium ..... ***Stagnicola*** (in part)

Gastropoda: Heterobranchia: Lymnaeiformes: Lymnaeidae: *Stagnicola:* Species

1	Prostate with two or more internal folds 2
1′	Prostate with a single internal fold 3
2(1)	Prostate with 5−10 internal folds (Fig. 11.11 I) ..... *Stagnicola* (*Corvusiana*) *corvus* (Gmelin, 1791) [Europe]
2′	Prostate with two internal folds (Fig. 11.11 J) ..... *Stagnicola* (*Corvusiana*) *fuscus* (C. Pfeiffer, 1821) [Europe]
3(1)	Penis sheath 1.5 times or longer than praeputium 4

3′	Penis sheath relatively short, length subequal to praeputium length (Fig. 11.11 F) ..... *Stagnicola* (*Stagnicola*) *palustris* (O.F. Müller, 1774) [widespread]
4(3)	ICA <0.25 (Fig. 11.11 H) ..... *Stagnicola* (*Stagnicola*) *saridalensis* (Mozley, 1934) [Kazakhstan, Russia]
4′	ICA = 0.30–0.60 (Fig. 11.11 G) ..... *Stagnicola* (*Stagnicola*) *turricula* (Held, 1836) [Europe]

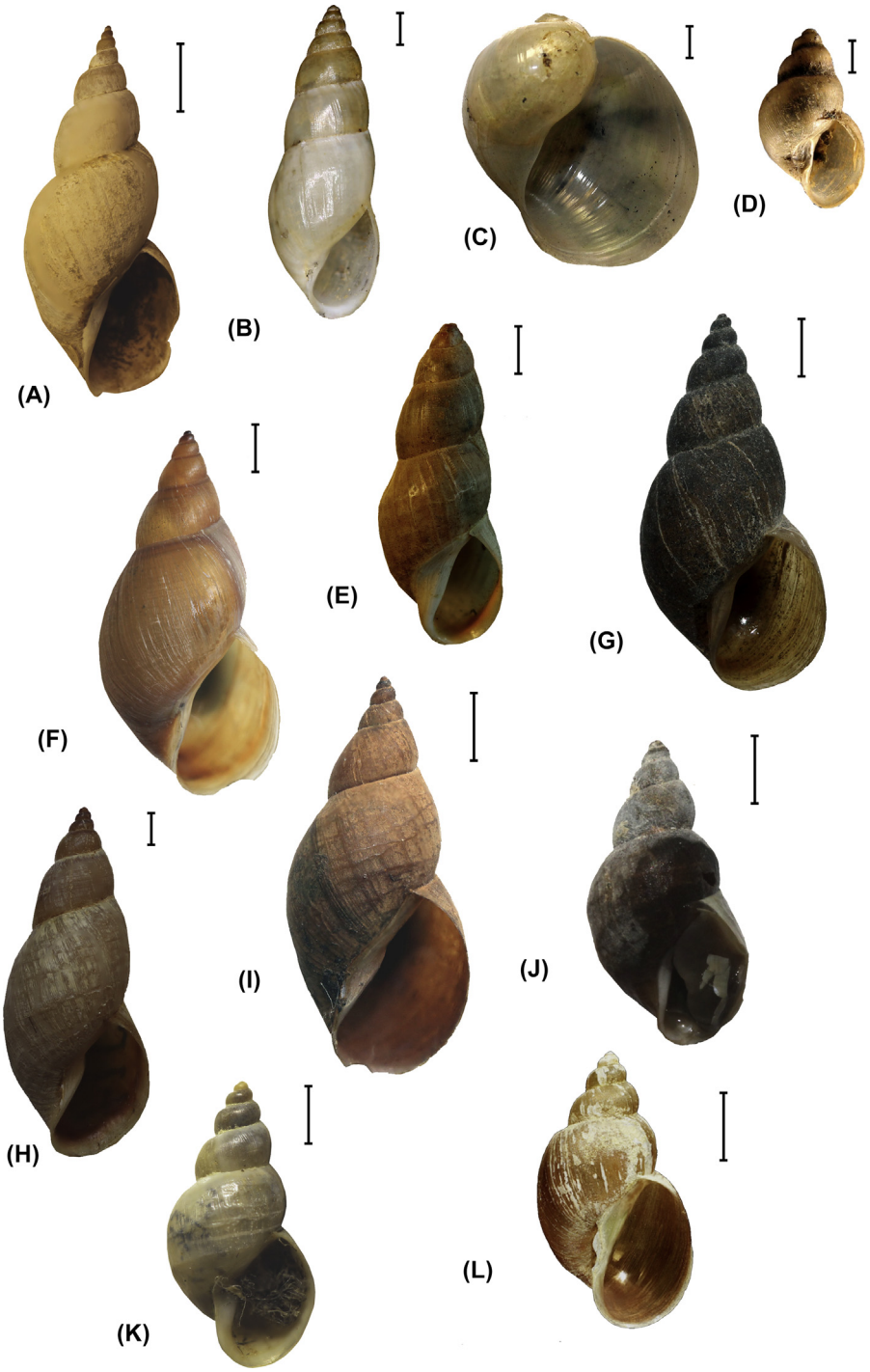


FIGURE 11.11 (A) *Lymnaea taurica*; (B) *Aenigmomphiscola europaea*; (C) *Myxas glutinosa*; (D) *Galba sibirica*; (E) *Ladislavella terebra*; (F) *Stagnicola palustris*; (G) *S. turricula*; (H) *S. saridalensis*; (I) *S. corvus*; (J) *S. fusca/vulnerata*; (K) *Galba truncatula*; and (L) G. *schirazensis*. Scale bars: 1 mm (D), 2 mm (B, C, E–H, K, and L), 5 mm (A, I, and J). *All photos are original, except L (after Glöer & Pešič, 2012).*

Gastropoda: Heterobranchia: Lymnaeiformes: Lymnaeidae: *Radix:* Species

We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1 Columellar depression prominent; spermathecal duct long and narrow 2

1′ Columellar depression weakly developed or absent; spermathecal duct short or absent 4

2(1) Adult shell auriciform, spire relatively short, along as strongly concave tangent-line 3

2′ Shell ovate-conical, spire high and almost straight (Fig. 11.12 C) ..... *Radix* (*Radix*) *parapsilia* Vinarski & Glőer, 2009 [eastern Palaearctic, eastern Europe]

3(2) Upper whorls strongly convex; columellar depression very deep; in large lakes (Fig. 11.12 D) *Radix* (*Radix*) *obliquata* (Martens, 1864) [central Asia]

3′ Upper whorls flattened or weakly convex; columellar depression moderate (Fig. 11.12 B) ..... *Radix* (*Radix*) *auricularia* (L., 1758) [Holarctic]

4(1) Shell not as below, SpH/SH ratio >0.25 5

4′ Shell auriciform, spire very low, SpH/SH ratio usually not exceeds 0.20 (Figs. 11.12 E, J) *Radix* (*Peregriana*) *ampla* (Hartmann, 1821) [Europe, Siberia]

..... *Radix* (*Peregriana*) *relicta* (Poliński, 1929) [Lake Ohrid]

..... *Radix* (*Peregriana*) *pinteri* Schütt, 1974 [Lake Prespa]

5(4) Shell high-conical; spire whorls unevenly rounded or flattened, if spire whorls evenly rounded then shell is <15 mm height with SpH/SH ratio not less than 0.35 6

5′ Shell shape varies from ovoid to ovate-conical; spire whorls evenly rounded; SpH/SH ratio 0.25−0.35 (Fig. 11.12 F) ..... *Radix* (*Peregriana*) *balthica* (L., 1758) [widespread]

6(5) Spire wide-conical, moderately high, tangent-line almost straight or weakly concave 7

6′ Spire relatively high and slender, tangent-line moderately concave (Fig. 11.12 I) ..... *Radix* (*Peregriana*) *lagotis* (Schrank, 1803) [central and western Palaearctic]

7(6) Shell relatively small, height usually <15 mm; whorls prominently convex; columellar lip narrow (Fig. 11.12 H) ..... *Radix* (*Peregriana*) *peregra* (O.F. Müller, 1774) [Europe]

7′ Shell larger, height to 20−22 mm; whorls weakly convex or flattened; columellar lip wide (Fig. 11.12 G) ..... *Radix* (*Peregriana*) *dolgini* (Gundrizer & Starobogatov, 1979) [Siberia and northern Far East]

Gastropoda: Heterobranchia: Lymnaeiformes: Lymnaeidae: *Orientogalba:* Species

1 Shell ovoid; spire relatively low with evenly convex whorls; body whorl very high, >0.80 total shell height (Fig. 11.12 K) ..... *Orientogalba viridis* (Quoy & Gaimard, 1833)

1′ Shell ovate-conical; spire high and slender, whorls strongly convex (almost stepped); body whorl ~0.70−0.80 total shell height (Fig. 11.12 L) ..... *Orientogalba heptapotamica* (Lazareva, 1967)

Gastropoda: Heterobranchia: Lymnaeiformes: Planorboidea: Families

We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1 Pseudobranch absent; shell obviously sinistral (coiling to the left), with an acute, posteriorly directed spire; mantle margin generally with digitate or serrate lobes; blood clear, lacking hemoglobin (Figs. 11.7 G−K) ..... **Physidae [p. 328]**

1′ Pseudobranch presents as a cup-like lobe projecting from under the mantle posteriolaterally on the left side; shell patelliform (limpets), discoidal (ram's horn snails), or if with a projecting spire, then appearing dextral (spiraling to the right) with spire blunt and and strongly convex whorls; blood red with hemoglobin (Figs. 11.4 A−F and 11.9 D−L) ..... **Planorbidae [p. 328]**

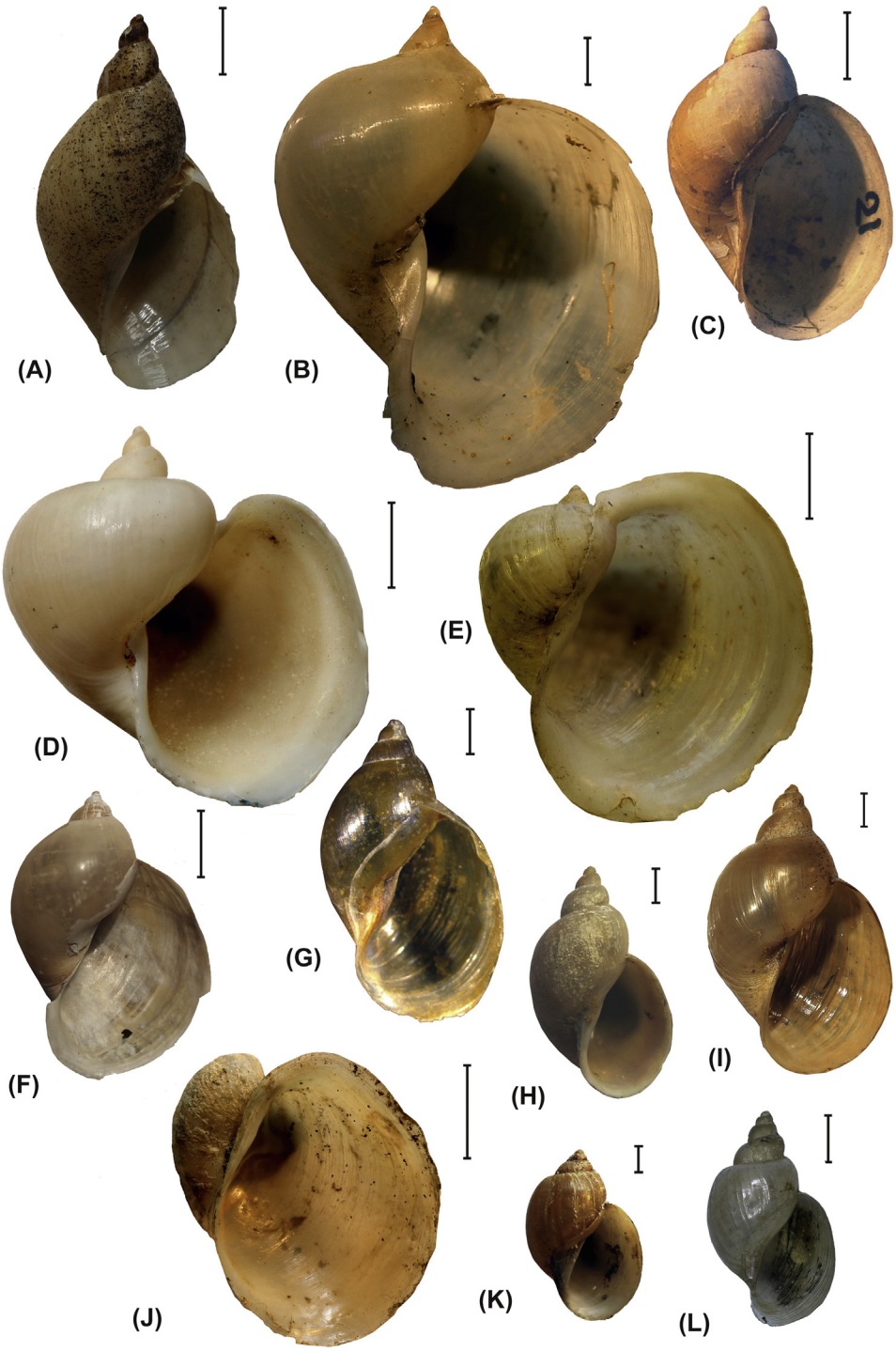


FIGURE 11.12 (A) *Pseudosuccinea columella*; (B) *Radix auricularia*; (C) *R. parapsilia*; (D) *R. obliquata*; (E) *R. ampla*; (F) *R. balthica*; (G) *R. dolgini*; (H) *R. peregra*; (I) *R. lagotis*; (J) *R. pinteri*; (K) *Orientogalba viridis*; and (L) *O. heptapotamica*. Scale bars: 2 mm (A, B, G–H, and J–K), 5 mm (C–F, and I). *All photos are original, except G, H, and J (after Vinarski et al., 2016).*

Gastropoda: Heterobranchia: Lymnaeiformes: Planorboidea: Physidae: Genera

Two subfamilies (Physinae s. str. and Aplexinae Starobogatov, 1967) are recognized, both represented in the Palaearctic. All are characterized by sinistral turbospiral shells that vary in shape from almost globose to high-turriculate. The Nearctic *Physa acuta* has become a prominent invasive species and is now distributed almost worldwide.

1	Shell with high elevated spire, turriculate, high conical, more or less slender; body whorl weakly or moderately inflated; subfamily Aplexinae 2
1′	Shell spire relatively low, body whorl greatly inflated and constituting most of shell volume; shell shape varies from conical to subglobose; subfamily Physinae ..... ***Physa*** **[p. 328]**
2(1)	Shell length to 20 mm; penis sheath divided into glandular portion and muscular portion ..... ***Sibirenauta*** [Siberia, northeast Palaearctic, North America]
2′	Shell length to 15 mm; penis sheath glandular, not divided (Fig. 11.10 A) ..... *Aplexa hypnorum* (L., 1758) [Palaearctic]

Gastropoda: Lymnaeiformes: Planorboidea: Physidae: *Sibirenauta:* Species

1	Shell slender, almost fusiform; spire oblong; body whorl moderately inflated (Fig. 11.10 B) ..... *Sibirenauta elongata* (Say, 1821)
1′	Shell ovate-conic; spire relatively short; body whorl prominently inflated (Fig. 11.10 C) ..... *Sibirenauta sibirica* (Westerlund, 1877)

Gastropoda: Lymnaeiformes: Planorboidea: Physidae: *Physa*: Species

1	Shell smaller, usually not higher than 10 mm, very fragile, semitransparent, with low spire and blunt apex 2
1′	Shell length to 15 mm, relatively solid, spire prominent, apex acute (Fig. 11.10 D) ..... *Physa acuta* (Draparnaud, 1805) [widespread invasive. Nearctic]
2(1)	Shell ovoid to almost globose, spire very low; SpH/SH ratio is 0.25 or less (Fig. 11.10 E) ..... *Physa fontinalis* (L., 1758) [Palaearctic]
2′	Shell ovate-conic, spire relatively prominent and narrow; SpH/H ratio is 0.30 or more (Fig. 11.10 F) ... *Physa taslei* Bourguignat, 1860 [Europe, Siberia, Mongolia]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: Genera

These pulmonates are distributed nearly worldwide (Starobogatov, 1970; Banarescu, 1990). The family includes several subfamilies, more than 30 genera and not less than 250 species (Strong et al., 2008) and is the most diverse basommatophoran family, both taxonomically and morphologically. Several species have been introduced through the aquarium trade (Glöer, 2002; Son, 2007; Sitnikova et al., 2010b; Welter-Schultes, 2012). We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell patelliform; subfamily Ancylinae 2
1′	Shell spiral 3
2(1)	Apex situated on shell longitudinal axis; maximum shell length to 5 mm, typically much smaller (Fig. 11.13 D) .... *Ferrissia fragilis* (Tryon, 1863) [widespread invasive. Nearctic]
2′	Apex situated on right side of shell longitudinal axis; shell typically larger than 5 mm ..... ***Ancylus*** **[p. 333]**
3(1)	Shell planispiral, always dextral 4
3′	Shell planispiral or turbospiral, but always sinistral; subfamily Bulininae 22
4(3)	Shell width typically less than 15 mm, if larger (up to 18–20 mm) then SH/SW ratio is about 0.20; subfamily Planorbinae 5
4′	Shell width 25–40 mm, if smaller (15–20 mm) then SH/SW ratio exceeds 0.25; tribe Coretini ..... ***Planorbarius*** **[p. 333]**
5(4)	Shell surface smooth, often softly shining, of lenticular or plano-convex shape 6
5′	Shell surface with more or less prominent sculpture (thin axial or spiral striae, streaks or riblets), not shining, discoidal 12
6(5)	Shell with three groups of whitish transverse lamellae within body whorl 7

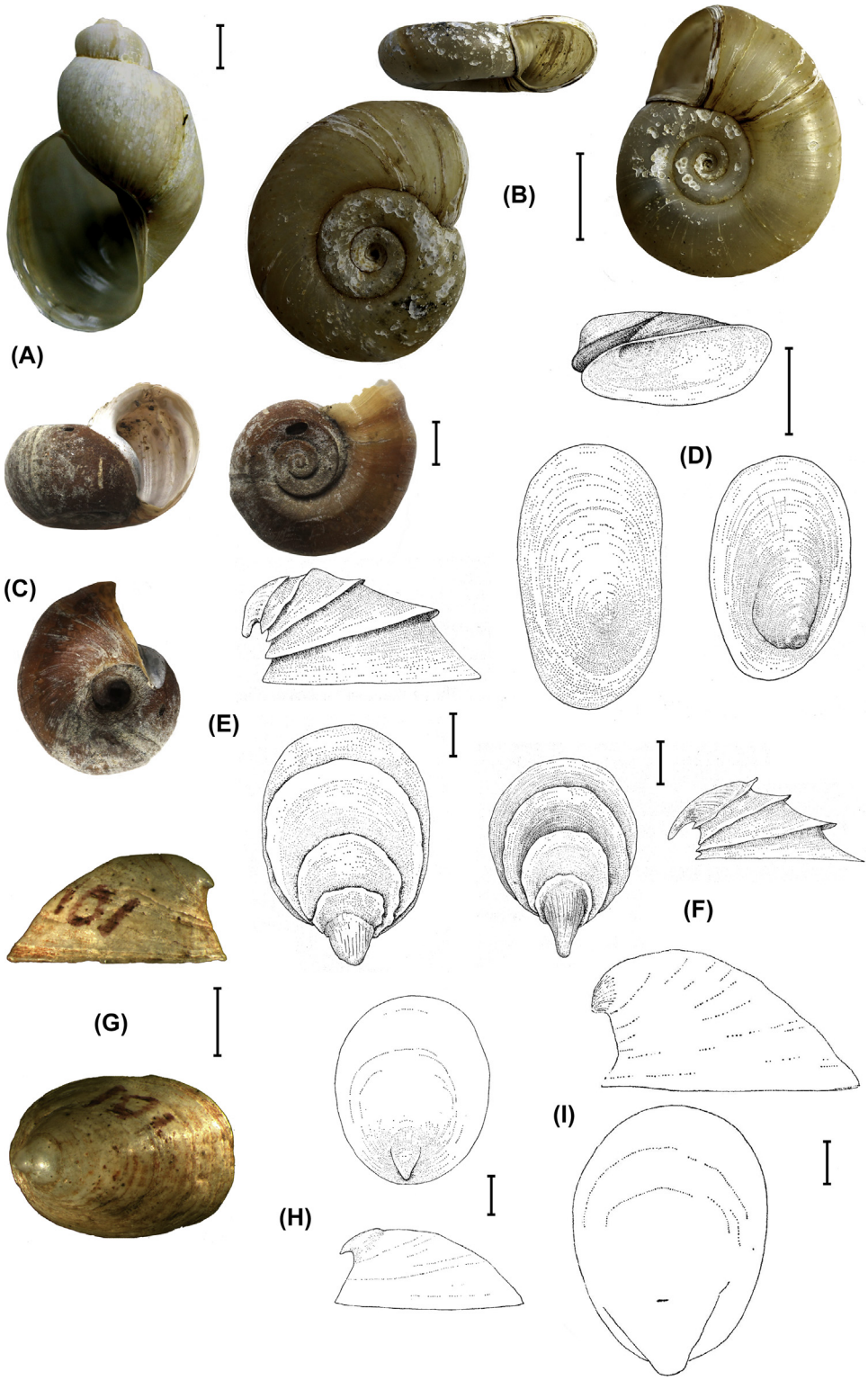


FIGURE 11.13 (A) *Bulinus truncatus*; (B) *Biomphalaria glabrata*; (C) *Planorbella anceps*; (D) *Ferrissia fragilis*; (E) *Ancylus lapicidus*; (F) *A. scalariformis*; (G) *A. fluviatilis*; (H) *A. tapirulus*; and (I) *A. benoitianus*. Scale bars 1 mm (E, F, H, and I), 2 mm (A, C, and G), 5 mm (B). *(E, F, H, and I) After Hubendick (1970); (G) after Nekhaev et al. (2015); (A–C) original photos.*

6′ Shell without internal lamellae 9

7(6) Umbilicus more or less wide, preceding whorls could be seen through it 8

7′ Umbilicus very narrow, sometimes spot-like..... *Trochorbis*
[central and eastern Asia]

8(7) Shell flattened, SH/SW ratio does not exceed 0.30 (Fig. 11.14 C) ..... *Segmentina*
[Europe, Iran, western Siberia]

8′ Shell semiglobular, SH/SW ratio not less than 0.34 (Fig. 11.14 D) ..... *Polypylis*
[central Asia, Siberia]

9(6) Shell colorless or light-yellow, silky shining; Europe, western Siberia 10

9′ Shell golden brown or golden yellow, glassy, shining; eastern Siberia, central Asia, and Far East 11

10(9) Shell width ≤3.5 mm; 2.5–3.5 whorls (Fig. 11.14 F) ..... *Lamorbis riparius* (Westerlund, 1865)
[Europe, western Siberia]

10′ Shell ≤6.0 mm; 4−5 whorls (Fig. 11.14 G) ..... *Hippeutis complanatus* (L., 1758)
[Europe, western Siberia]

11(9) Shell very small, width ≤3.5 mm (Fig. 11.14 E) ..... *Kolhymorbis* Starobogatov & Streletzkaja, 1967
[eastern Siberia, Far East, and Tajikistan]

11′ Shell width ≥4.0 mm (Fig. 11.14 H) ..... *Helicorbis kozhovi* Starobogatov & Streletzkaja, 1967
[Siberia, Mongolia]

12(5) Upper shell surface flat or convex 13

12′ Upper surface concave 17

13(12) Upper shell surface flat, not elevated 14

13′ Initial whorls more or less elevated above body whorl; prominent spire sometimes developed (Figs. 11.14 I, J) .....
..... *Choanomphalus* (in part)
[Lake Baikal and adjacent areas, Far East, Mongolia]

14(13) Body whorl angulated or keeled; whorls 3.0−3.5 15

14′ Body whorl not angulated or keeled 16

15(14) Shell ≥3.0 mm. ..... ***Armiger***
[central Asia, Europe, Siberia]

15′ Shell <3.5 mm. ..... *Menetus*
[invasive. Nearctic region]

16(14) Shell with 3.5−4.5 rapidly increasing whorls; width rarely exceeds 8−10 mm 19

16′ Shell with 5.0−7.0 (rarely more) slowly increasing whorls, if fewer (4.5−5.0) then width ≤ 8−10 mm. 20

17(12) Shell width 10.0−25 mm; whorls 3.0−4.0 18

17′ Shell width ≤ 4.0 mm; whorls 3.0−3.5 ..... *Choanomphalus* (in part)
[Lake Baikal]

18(17) Shell thin, fragile (Fig. 11.13 B) ..... *Biomphalaria*
[north Africa. Invasive in Europe and Asia. Nearctic, Neotropical regions]

18′ Shell thick, not easily crushed (Fig. 11.13 C) ..... *Helisoma*
[invasive via the aquarium trade. Nearctic region]

19(16) Shell surface bears regular axial sculpture represented by prominent, dense riblets; aperture rounded, lip often whitish (Fig. 11.14 K)
..... *Lamorbis rossmaessleri* (Auerswald in A. Schmidt, 1851)
[Europe, Siberia]

19′ Shell surface almost smooth or striated but lacking axial riblets; aperture more or less oblong, without whitish lip .....
.....***Gyraulus*** **[p. 336]**

20(16) Shell with definitive width rarely exceeding 10 mm (SH/SW ratio >0.14); penis sheath thick and distally tumid 21

20′ Shell with definitive width ≥10 mm, if less than 10 mm, then penis sheath much narrower than praeputium and not distally tumid; SH/SW ratio typically ≥0.18–0.25 ..... ***Planorbis*** **[p. 334]**

21(20) Umbilicus deep and broad; whorls in dorsal view very narrow; aperture width significantly less than its height (Fig. 11.15 A) .....
..... *Bathyomphalus contortus* (L., 1758)
[widespread in Palaearctic]

21′ Umbilicus shallow and broad; whorls in dorsal view not narrow; aperture width greater than aperture height ..... ***Anisus*** **[p. 334]**

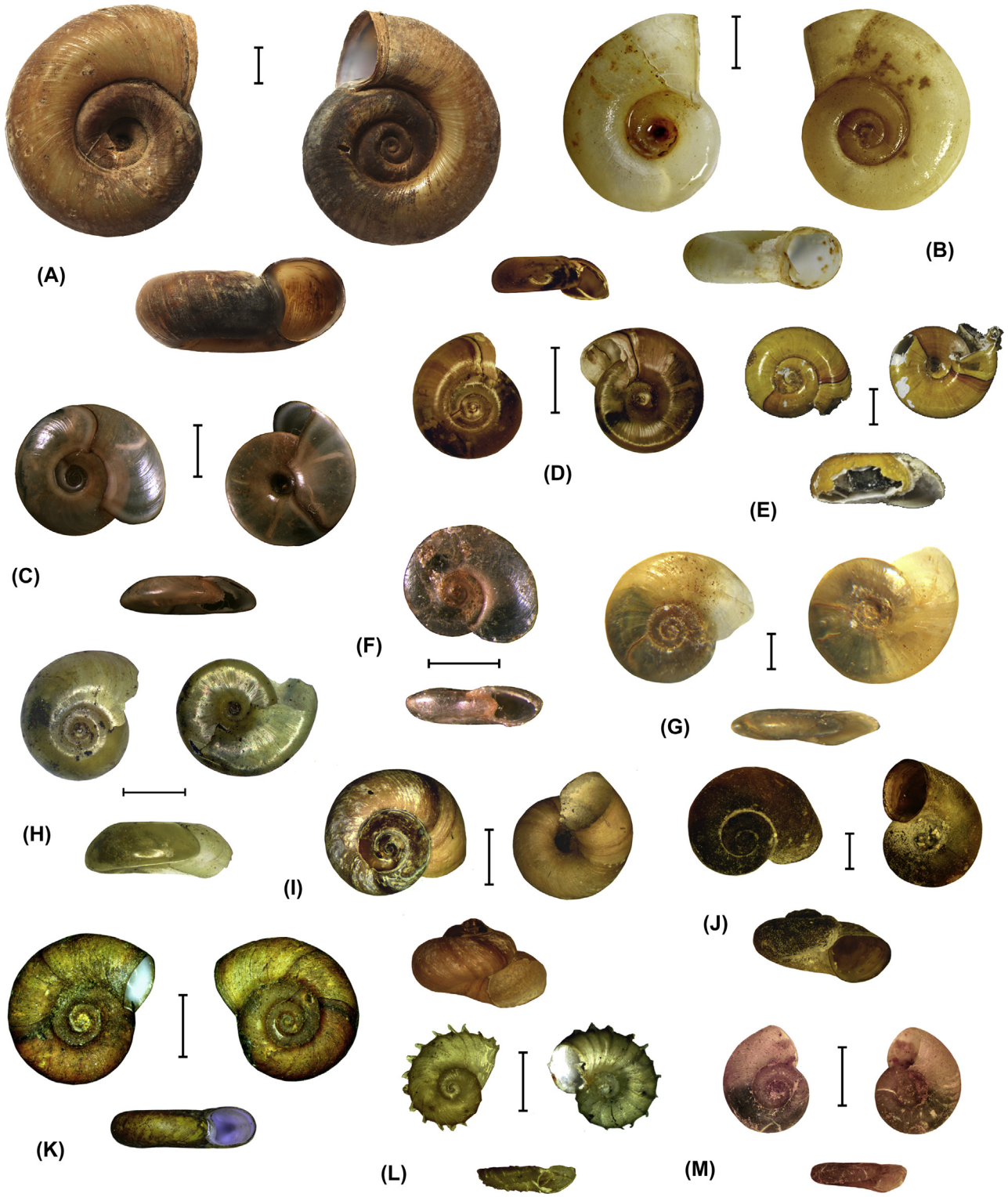


FIGURE 11.14 (A) *Planorbarius corneus*; (B) *P. metidjensis*; (C) *Segmentina nitida*; (D) *Polypylis sibirica*; (E) *Kolhymorbis shadini*; (F) *Lamorbis riparius*; (G) *Hippeutis complanatus*; (H) *Helicorbis kozhovi*; (I) *Choanomphalus maacki*; (J) *Choanomphalus mongolicus*; (K) *Lamorbis rossmaessleri*; (L) *Armiger crista*; and (M) *A. bielzi*. Scale bars: 1 mm (E, F, and J), 2 mm (C, D, G–I, and K), 5 mm (A and B). *All photos are original, except E—after Sitnikova et al. (2014), slightly modified.*

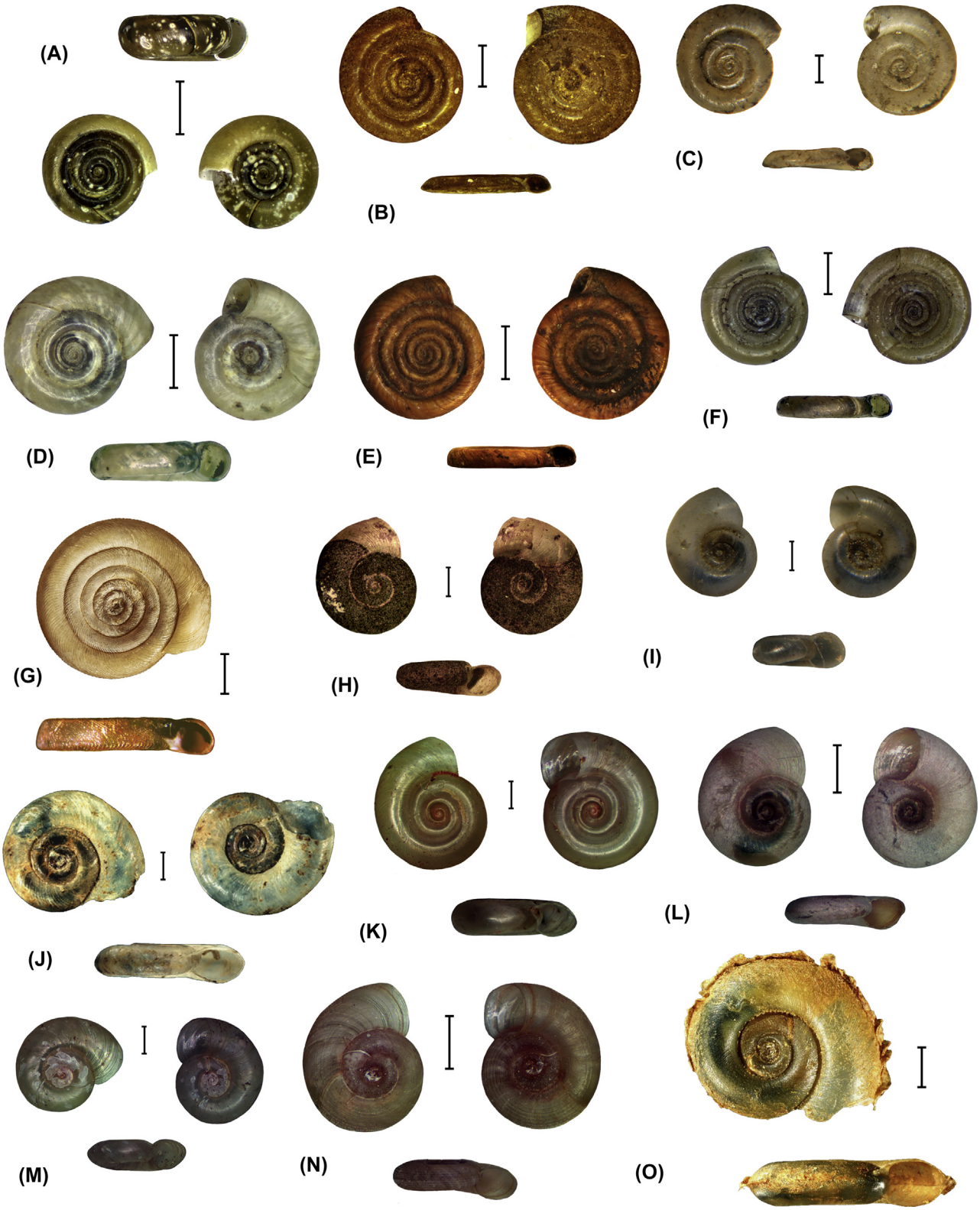


FIGURE 11.15 (A) *Bathyomphalus contortus*; (B) *Anisus vortex*; (C) *A. vorticulus*; (D) *A. spirorbis*; (E) *A. septemgyratus*; (F) *A. leucostoma*; (G) *A. strauchianus*; (H) *Gyraulus parvus*; (I) *G. laevis*; (J) *G. hebraicus*; (K) *G. convexiusculus*; (L) *G. piscinarum*; (M) *G. ehrenbergi*; (N) *G. albus*; and (O) *G. stroemi*. Scale bars: 1 mm (C, H–K, and M), 2 mm (A, B, D–G, L, N, and O). *All photos are original except G (photo, D. Palatov), J (after Glöer & Bössneck, 2007), O (after Glöer & Vinarski, 2009).*

22(3) Shell turbospiral (Fig. 11.13 A) ..... *Bulinus truncatus* (Audouin, 1828)
[north Africa, Portugal, Sardinia. Afrotropical]

22′ Shell planospiral ..... *Indoplanorbis. exustus* (Deshayes, 1834)
[Afghanistan, Iran, Iraq, Pakistan; widely distributed in south and southeast Asia]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Ancylus*: Species

This key is based on morphological data presented by Hubendick (1970) and Soldatenko & Starobogatov (2004). Several nominal species reported from south Europe and the Caucasian region may represent valid species but their taxonomic status needs to be reassessed. Some authors accept them as valid (Soldatenko & Starobogatov, 2004; Soldatenko, 2009), other regard them as synonyms of *A. fluviatilis* (Hubendick, 1970; Welter-Schultes, 2012).

1 Shell with prominent concentric ribs or lateral projections below apical region, occurring in Lake Ohrid 2

1′ Shell without concentric ribs, nearly smooth or with weak striation 3

2(1) Apical region relatively slender and obviously sculptured, with prominent longitudinal ridges (Fig. 11.13 E) ..... *Ancylus lapicidus* Hubendick, 1960

2′ Apical region broad, weakly sculptured, with about 20 thin axial striae, never ridges (Fig. 11.13 F) *Ancylus scalariformis* Stanković & Radoman, 1953

3(1) Apex shifted nearly to shell posterior margin and often situated outside aperture outline 4

3′ Apex situated away from shell posterior margin and always situated inside aperture outline (Fig. 11.13 G) ..... *Ancylus fluviatilis* O.F. Müller, 1774
[Europe, northern Africa]

4(3) Apical region cornet-shaped and slender (Fig. 11.13 H) ..... *Ancylus tapirulus* Poliński, 1929
[Lake Ohrid]

4′ Apical region relatively short and broad (Fig. 11.13 I) ..... *Ancylus benoitianus* Bourguignat, 1853
[Mediterranean, Transcaucasia]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Planorbarius*: Species

1 Adult shell ≥20 mm width; first whorls depressed dorsally and ventrally (Fig. 11.14 A) ..... *Planorbarius corneus* (L., 1758)
[Europe (except Iberia), western Siberia]

1′ Adult shell ≤16 mm; first whorls depressed apically only, ventral surface flattened (shell sinistral, with aperture on left) (Fig. 11.14 B) ..... *Planorbarius metidjensis* (Forbes, 1838)
[southwestern Europe, northern Africa]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Armiger*: Species

1 Spire not prominent and usually not elevated above the body whorl surface; sculpture, if present, represented by dense ribs or spines 2

1′ Spire prominent and elevated above the body whorl surface (Fig. 11.16 N); sculpture represented by not very prominent and well-spaced obtuse ribs ..... *Armiger annandalei* (Germain, 1918)
[Afghanistan, Mongolia, Russia (Tuva)]

2(1) Aperture palatal margin straight, peripheral angle shifted toward dorsal surface (Fig. 11.14 L) ..... *Armiger crista* (L., 1758)
[Holarctic]

2′ Aperture palatal margin arcuate, peripheral angle situated between upper and lower shell surfaces (Fig. 11.14 M) ..... *Armiger bielzi* (Kimakowicz, 1884)
[northern Eurasia]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Planorbis*: Species

This key is based partially on Soldatenko & Starobogatov (2000) and Glöer & Pešič (2010).

1	Umbilicus wide and relatively shallow, discoidal 2
	Umbilicus deep and conical (Fig. 11.16 F) ..... *Planorbis presbensis* Sturany, 1894 [Macedonia (Prespa Lake)]
2(1)	Adult shell >12 mm; keel well developed, if periphery of shell weakly keeled or angled, then shell width >10 mm; Europe, Siberia 3
2′	Adult shell <10 mm; shoulder rounded or angled; keel usually weakly developed or absent; southern Europe, Near East, Central Asia 4
3(2)	Keel situated between dorsal and ventral shell surfaces; aperture rhomboid; prostate with 23−32 diverticles (Fig. 11.16 H) .. *Planorbis carinatus* (O.F. Müller, 1774) [Europe]
3′	Keel shifted toward ventral surface; aperture oval; prostate with 35−57 diverticles (Fig. 11.16 I) ..... *Planorbis planorbis* (L., 1758) [Europe, northern Africa, Near East, western Siberia]
4(2)	Umbilicus wide and deep; ventrally, initial whorls depressed 5
4′	Umbilicus shallow; ventrally, initial whorls not significantly depressed 6
5(4)	Prostate with 21−26 diverticles (Fig. 11.16G) .....*Planorbis tangitarensis* Germain, 1918 [central Asia]
5′	Prostate with 29−32 diverticles (Fig. 11.16 D) ..... *Planorbis macedonicus* Sturany, 1894 [Ohrid Lake]
6(4)	Shell width ≤10 mm; prostate with 20−36 diverticles (Fig. 11.16 K) Prostate with 29−32 diverticles ..... *Planorbis intermixtus* Mousson, 1874 [Greece to central Asia]
6′	Shell ≤8.5 mm; prostate with 16−26 diverticles (Fig. 11.16 M) .....*Planorbis atticus* Bourguignat, 1852 [eastern Mediterranean region. Caucasia?]

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Anisus*: Species

1	Shell keeled or angled, fragile, relatively thin 2
1′	Shell periphery more or less evenly rounded; shell relatively solid, without keel or prominent angle 3
	2(1) Shell with prominent keel, aperture rhomboid, shell width 6−10 mm (Fig. 11.15 B) ..... *Anisus* (*Disculifer*) *vortex* (L., 1758) [Europe, Siberia]
2′	Shell not keeled, with peripheral angle more or less prominent or with a narrow, thin periostracal fringe; shell width ≤5 mm (Fig. 11.15 C) ..... *Anisus* (*Vorticulus*) *vorticulus* (Troschel, 1834) [Europe, western Siberia]
3(1)	Shell surface without riblets 4
3′	Shell surface covered by thin and prominent radial riblets (Fig. 11.15 G) ..... *Anisus* (*Costorbis*) *strauchianus* (Clessin, 1884) [eastern Europe]
4(3)	Whorls >6.0; SH/SW ratio <0.25; prostate diverticles ≥20 5
4′	Whorls <5.5; SH/SW ratio 0.25–0.28; prostate diverticles 10–15 (Fig. 11.15 D) ..... *Anisus* (*Anisus* s. str.) *spirorbis* (Linnaeus, 1758) [Europe, Siberia]
5(4)	Shell very flat, SH/SW ratio 0.14–0.18; whorls 7.5–8.5; prostate bears 30–50 or more diverticles (Fig. 11.15 E) .... *Anisus* (*Anisus* s. str.) *septemgyratus* (Rossmässler, 1835) [Europe]
5′	SH/SW ratio 0.20–0.23; whorls ≤6.5; prostate with 20−25 diverticles (Fig. 11.15 F) .... *Anisus* (*Anisus* s. str.) *leucostoma* (Millet, 1813) [Europe, Siberia]

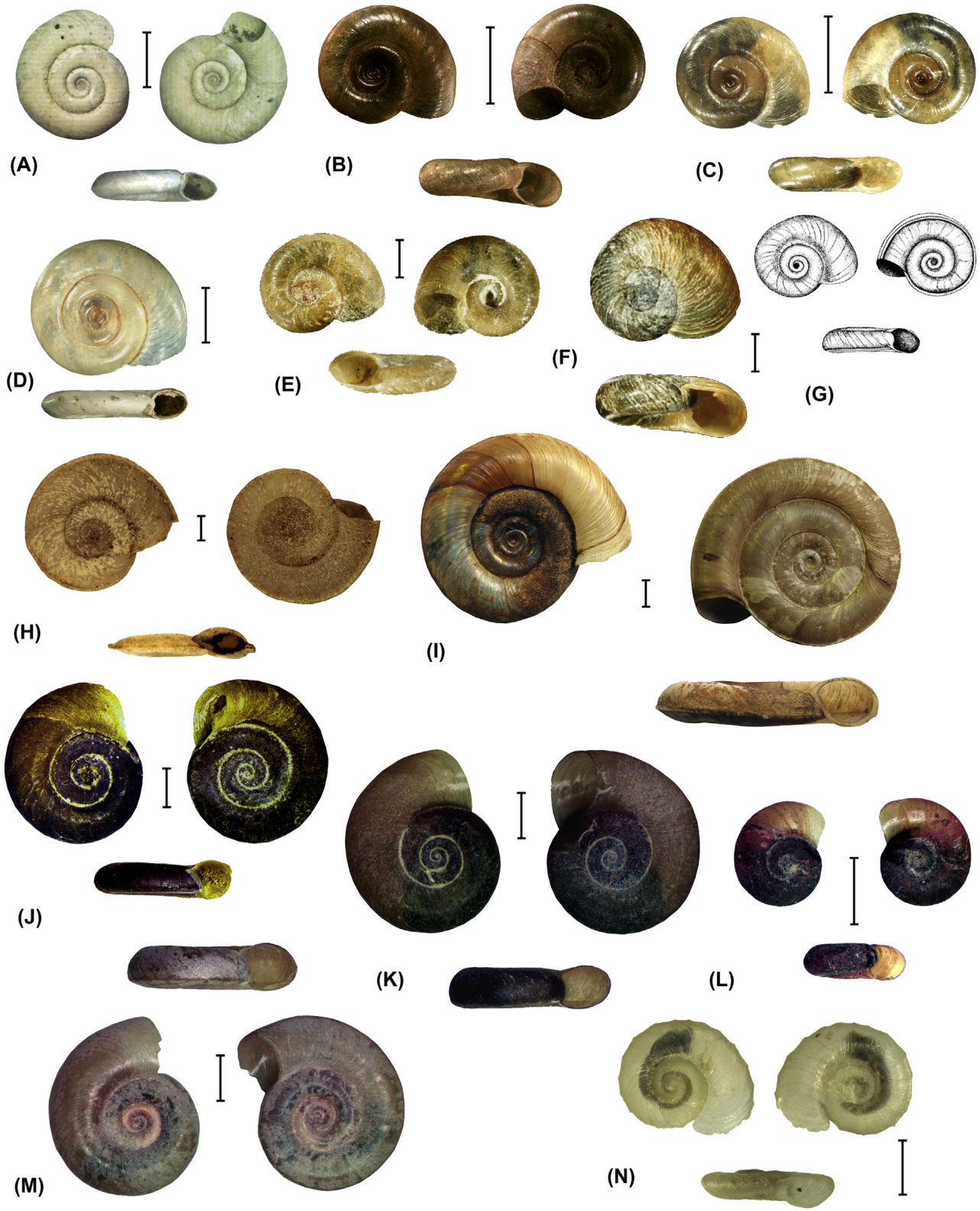


FIGURE 11.16 (A) *Gyraulus acronicus*; (B) *G. borealis*; (C) *G. chinensis*; (D) *G. euphraticus*; (E) *G. argaeicus*; (F) *Planorbis presbensis*; (G) *P. tangitarensis*; (H) *P. carinatus*; (I) *P. planorbis*; (J) *P. macedonicus*; (K) *P. intermixtus*; (L) *P. agraulus*; (M) *P. atticus*; and (N) *Armiger annandalei*. Scale bars 2 mm (except G—5 mm). *All pictures are original, except B (photo, I. Nekhaev), C (photo, P. Glöer), D (after Glöer & Bössneck, 2007, slightly modified), E (after Glöer & Georgiev, 2012, slightly modified), F (Glöer & Pešič, 2010a, slightly modified), G (after Subba Rao, 1989).*

Gastropoda: Lymnaeiformes: Planorboidea: Planorbidae: *Gyraulus:* Species

Many nominal *Gyraulus* species have been recently described from Europe, the Near East, and Siberia (Prozorova & Starobogatov, 1997; Prozorova, 2003; Glöer & Pešić, 2007; Glöer & Georgiev, 2012; and others). However, their validity is still in question, and they are not included here. These keys follow Zhadin (1952), Meier-Brook (1983), and Welter-Schultes (2012). We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell planispiral, umbilicus relatively wide and shallow, if deep, then not accompanied by angle or keel 2
1′	Shell nonplanispiral, umbilicus deep and conical, delimited by an angle or keel; from large ancient Balkan lakes subgenus *Carinogyraulus*
2(1)	Adult shell width <5 mm, smooth and glossy 3
2′	Adult shell width 7−10 mm, if smaller, then the surface bears more or less prominent spiral or reticular sculpture 8
3(2)	Prostate diverticula mostly irregular and closely spaced; Europe 4
3′	Prostate diverticula regular and closely spaced. Near East, Central Asia, southeastern Europe 5
4(3)	Penultimate whorl distinctly elevated; body whorl prominently deflected (Fig. 11.15 H) ..... *Gyraulus* (*Torquis*) *parvus* (Say, 1817) [invasive in central Europe. Nearctic]
4′	Penultimate whorl not or marginally elevated; body whorl not deflected (Fig. 11.15 I) ..... *Gyraulus (Torquis) laevis* (Alder, 1838) [Europe]
5(3)	Umbilicus wide and deep 6
5′	Umbilicus narrow and rather shallow 7
6(5)	Body whorl dorsally slightly ribbed; SW/SH ratio ∼3.5−4.1 (Fig. 11.15 L) ..... *Gyraulus* (*Gyraulus*) *piscinarum* (Bourguignat, 1852) [Bulgaria (Skadar Lake), Near East]
6′	Body whorl dorsally not ribbed; SW/SH ratio ∼4.5 (Fig. 11.15 K) ..... *Gyraulus* (*Gyraulus*) *convexiusculus* (Hutton, 1849) [central Asia]
7(5)	SW/SH ratio ∼4.0; prostate with 11−15 diverticles (Fig. 11.15 J) ..... *Gyraulus* (*Gyraulus*) *hebraicus* (Bourguignat, 1852) [Near East]
7′	SW/SH ratio ∼4.5; prostate with 14−19 diverticles (Fig. 11.15 M) ..... *Gyraulus* (*Gyraulus*) *ehrenbergi* (Beck, 1837) [northern Africa, Near East]
8(2)	Shell without spiral sculpture or with sculpture almost invisible or represented by thin spiral striae, most prominent on initial whorl surface 9
8′	Shell with coarse spiral sculpture represented by more or less prominent ribs (Fig. 11.15 N) ..... *Gyraulus* (*Gyraulus*) *albus* (O.F. Müller, 1774) [Europe, Siberia]
9(8)	Shell width < 8 mm; periostracal fringe absent or weakly developed; Europe, Near East, central Asia 10
9′	Shell width 8−10 mm; periostracal fringe wide and situated midway between dorsal and ventral shell surfaces (Fig. 11.15 O) ..... *Gyraulus* (*Gyraulus*) *stroemi* (Westerlund, 1881) [north Europe, Siberia]
10(9)	Shell width to 7 mm; prostate with 20−40 diverticles; Europe, Siberia 11
10′	Shell width to 5 mm, if larger (5−7 mm), then prostate with 9−22 diverticles; Near East, central Asia 12
11(10)	Shell peripheral angle weakly keeled, last whorl more or less deflected; SH/SW ratio usually <0.25 (Fig. 11.16 A) ..... *Gyraulus* (*Gyraulus*) *acronicus* (Férussac, 1807) [Europe (except north and south), Siberia]
11′	Shell peripheral angle evenly rounded, last whorl not or weakly deflected; SH/SW ratio >0.25 (typically 0.26−0.31) (Fig. 11.16 B) ..... *Gyraulus* (*Gyraulus*) *borealis* (Lovén in Westerlund, 1875) [northern Europe, Siberia]
12(10)	Shell width up to 7 mm; shell peripheral angle slightly keeled; Near East 13
12′	Shell width up to 5 mm; shell peripheral angle rounded (Fig. 11.16 C) ..... *Gyraulus* (*Gyraulus*) *chinensis* (Dunker, 1848) [Central Asia. Invasive in Europe]
13(12)	Umbilicus narrow; SH/SW ratio ≥0.20 (Fig. 11.16 D) ..... *Gyraulus* (*Gyraulus*) *euphraticus* (Mousson, 1874)
13′	Umbilicus wide and deep; SH/SW ratio ∼0.15 (Fig. 11.16 E) ..... *Gyraulus* (*Gyraulus*) *argaeicus* (Sturany, 1904)

Gastropoda: Neritimorpha: Neritidae: Genera

Two genera enter Palaearctic freshwaters. *Theodoxus* is rather widespread, with representatives in the Baltic Sea Basin (though absent in Siberia), but most species are restricted to the Mediterranean region and the Near East. Nearly 20 species are currently accepted in Europe and Asia Minor (Welter-Schultes, 2012), three species are endemics to northern Africa (Brown, 1994). There are endemic species in the Near East (Glöer & Pešić, 2012). Shell size, proportions, and patterns of shell coloration may be utterly misleading, with shell surface coloration and banding patterns varying under different environmental conditions (Fehér et al., 2009; Glőer & Pešić, 2015). Thus, there are some doubts on validity of some southern European *Theodoxus* species with extremely local distributions (Welter-Schultes, 2012; Glőer & Pešić, 2015).

Neritina is mostly marine, with a few species entering freshwater in the western Palaearctic. The primary difference between the two is that *Neritina* has free-swimming planktonic larvae, whereas *Theodoxus* juveniles hatch as miniature versions of the adults.

1 Operculum inside surface with single apophysis (Figs. 11.1 E–K) ..... *Theodoxus*

1′ Operculum inside surface with two apophyses ..... *Neritina*
[Iran, Iraq]

Gastropoda: Caenogastopoda: Families

This group contains the greatest diversity among Holarctic freshwater gastropods. Those families of the Hydrobidoidea are not identified further than superfamily, and includes Amnicolidae [two genera of this family are most widely distributed in Palaearctic—*Marstoniopsis* van Regteren Altena, 1936 (Europe; Fig. 11.2 I) and *Kolhymamnicola* (northeastern Siberia eastward to Chukotka Peninsula; Fig. 11.2 J)], Bythinellidae (Figs. 11.1 C, D), Hydrobiidae s. str., and Moitessieriidae. Representatives of these families have overlapping shell characters, and it is impossible to develop a strictly morphological key for their determination. Most differences between these families lie in genetics and internal anatomy, including stucture of radulae, genital, digestive, and excretory systems (see Radoman, 1983; Starobogatov & Sitnikova, 1983; Boeters et al., 2013).

1 Shell of different size and/or shape 2

1′ Shell planispiral, width up to 5 cm, with 3–6 dark spiral stripes ..... Ampullariidae, one species: *Marisa cornuarietis* (L., 1758)
[neotropical. Invasive in Hungary, Spain]

2(1) Shell definitive size 20 mm or less, if larger then body whorl without dark bands 3

2′ Shell relatively large, definitive size not less than 25 mm height (up to 30–35 mm), usually with three dark bands on body whorl ..... **Viviparidae [p. 338]**

3(2) Shell of other shape, if aperture rounded then shell height exceeds 10 mm 4

3′ Shell valvatoid (Fig. 11.1 B) or planispiral, with perfectly round or rounded aperture; shell height <10 mm, width <2.2 mm; subterranean and in springs and other minor and shallow waterbodies ..... Hydrobiidoidea (in part)

4(3) Shell not as below, if ovate-conical then apertural margin not widened 5

4′ Shell ovate-conical, relatively small (up to 10 mm height), with wide base, apertural margin greatly and sometimes slightly turned aside (Fig. 11.1 A) ..... Emmericiidae, one genus: *Emmericia*
[Balkans, Italy. Invasive France, Germany]

5(4) Shell globose to high turriculate, its height varies greatly but usually >10 mm (up to 45 mm in some species); endemic to Baikal Lake 6

5′ Species range not limited to Baikal Lake and Angara River basin 7

6(5) Shell height at four whorls exceeds 8 mm except of three "dwarf" species that inhabit Baikal Lake at depths 50–420 m ..... **Benedictiidae [p. 339]**

6′ Shell height at four whorls <6 mm (Figs. 11.2 K–S) ..... Baicaliidae

7(5) Shell not turriculate, or if turriculate then shell surface not sculptured or shell height <10 mm; whorls number never more than nine (except of some eastern Mediterranean Melanopsidae) 8

7′ Shell turriculate, often sculptured, elongate (SH/SW ratio not less than 2.5), with four or more (usually 10–15) very slowly increasing whorls 13

8(7) Shell not as below, if turriculate or ovate-conical then height ≤12 mm 9

8′ Shell turriculate (not sculptured) or ovate-conic; shell height exceeds 12 mm ..... **Melanopsidae**
[southern Europe, Near East, central Asia]

9(8) Shell not globose or low conical, otherwise aperture not widened 10

9′ Shell almost globose or low conical, with short spire and relatively wide ovoid aperture; shell height 7–12 mm ..... Lithoglyphidae, one genus: ***Lithoglyphus* [p. 340]**

10(9) Shell height 5–12 mm 11

10′ Shell height does not exceed 5 mm (typically < 3–4 mm) ..... Hydrobiidoidea (in part)

11(10)	Shell oblong, turriculate or high conical	12
11′	Shell ovate conical, ovoid or low conic; operculum with a few or numerous concentric striae and central elliptic "nucleus"	**Bithyniidae [p. 341]**
12(11)	Shell high conic, height not exceeding 6 mm, not keeled or with a single weakly developed keel (Fig. 11.4 B) fresh and brackish water	Tateidae, one species: *Potamopyrgus antipodarum* (Gray, 1843) [invasive, widespread in Europe]
12′	Shell turriculate or highly conical, usually prominently keeled, height to 10 mm	Hydrobiidae subfamily Pyrgulinae [southern Europe, Ponto-Caspian region, including Azov and Black Seas]
13(7)	Shell variable; freshwater systems, never in mangrove estuaries	14
13′	Shell heavily sculptured, aperture flared; occurring in mangrove estuaries	Potamididae, one species: *Cerithidea cingulata* (Gmelin, 1790) [Indian Ocean coast]
14(13)	Mantle margin papillate	**Thiaridae** [southern Palaearctic. introduced in central Europe]
14′	Mantle smooth	**Semisulcospiridae [p. 340]**

Gastropoda: Caenogastopoda: Viviparidae: Genera

Viviparid snails, with shells that may reach 35 mm, are the largest native Palaearctic branchiate gastropods (apart from Benedictiidae, Baikal Lake endemics, which may exceed 44 mm). Viviparids are dioecious and viviparous. The male right tentacle is modified as a copulatory organ. This family is widely represented in the Palaearctic (except eastern Siberia and extreme northeast Asia), the Nearctic and Afrotropical regions. Most Palaearctic species belong to *Viviparus* Montfort, 1810. Two species of the tropical genus *Bellamya* are known to occur in some southern regions of the Palaearctic (Egypt, Iraq, Iran). These keys are based on the work of Glőer & Georgiev (2014) with some additions and changes. The authors state that in some *Viviparus*, the characters of embryonic or juvenile shells are most suitable for specific determination.

These keys are for adult animals (more than three body whorls, dark periostracum) only. We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell relatively slender, with high spire and weakly inflated body whorl	2
1′	Shell not slender (ovate-conical to almost globose), spire low or medium-sized, body whorl usually prominently inflated	4
2(1)	Whorls rounded, shoulder flattened or rounded	3
2′	Whorls and shoulders obviously flattened	*Heterogen longispira* Annandale, 1921 [Japan]
3(2)	Shell long, conical; whorls flatly convex; shell thick	*Sinotaia* [China]
3′	Shell ovate conical; whorls rounded; shell thin (Fig. 11.5 A)	*Bellamya* [widespread. Widely introduced]
4(1)	Operculum oval	*Bellamya* [widespread. Widely introduced]
4′	Operculum subcircular	***Viviparus*** [widespread]

Gastropoda: Caenogastopoda: Viviparidae: *Viviparus:* Species

1	Apex acute (may be tested with fingertip)	2
1′	Apex blunt (test with fingertip) (Fig. 11.5 B)	*Viviparus* (*Viviparus*) *viviparus* (Linnaeus, 1758) [Europe, Caucasus, introduced to western Siberia]
2(1)	Whorls slightly convex and not stepped	3
2′	Whorls convex and stepped (Fig. 11.5 C)	*Viviparus* (*Contectiana*) *contectus* (Millet, 1813) [Europe, western Siberia]
3(2)	Body whorl rounded, shell height >22 mm	4
3′	Body whorl canted, shell height <22 mm, embryonic shells glaborous (Fig. 11.5 D)	*Viviparus* (*Contectiana*) *hellenicus* (Clessin, 1879) [southern Europe]

4(3) SpH/SH ratio >0.24; shell height >28 mm 5

4′ First whorls flat, SpH/SH ratio 0.21, shell height <28 mm (Fig. 11.5 E) ..... *Viviparus* (*Contectiana*) *sphaeridus* (Bourguignat, 1862)
[lower Danube, Dnieper, and Dniester river basins]

5(4) Juvenile body whorl rounded, embryonic shell with hairs 6

5′ Juvenile body whorl slightly canted, embryonic shells without or with very small hairs (Fig. 11.5 F) ..... *Viviparus* (*Contectiana*) *ater* (Cristofori & Jan, 1832)
[central and parts of southern Europe]

6(5) First whorls flat and slightly flattened at the suture (Fig. 11.5 G) ..... *Viviparus* (*Contectiana*) *mamillatus* (Küster, 1852)
[southern Europe]

6′ Whorls not flattened at the suture (Fig. 11.5 H) ..... *Viviparus* (*Contectiana*) *acerosus* (Bourguignat, 1862)
[central and eastern Europe]

Gastropoda: Caenogastopoda: Benedictiidae: Genera and Subgenera

This key is based on Sitnikova (1995). Limited to Lake Baikal.

1 Shell 8−13 mm height with 3.5−4 whorls 2

1′ Shell less than 7 mm but more than 14 mm in height with 3.5−4 whorls 3

2(1) SpH/AH ratio >0.70; whorls shouldered, with deep sutures (Fig. 11.6 A) ..... *Kobeltocochlea* (*Pseudobenedictia*)

2′ SpH/AH ratio <0.68; whorls flattened, with shallow sutures (Fig. 11.6 B) ..... *Kobeltocochlea* sensu stricto

3(1) Shell with shouldered or well-rounded whorls with deep sutures (Fig. 11.6 C) ..... *Benedictia* (*Baicalocochlea*)

3′ Shell with flattened or oval-rounded whorls and shallow or indented sutures (Fig. 11.3 D) ..... *Benedictia* sensu stricto

Gastropoda: Caenogastopoda: Thiaridae: Genera

This family occurs across the southern Palaearctic and through the tropics (Starobogatov, 1970), with an overall diversity of about 135 species (Strong et al., 2008). One species, *Melanoides tuberculata*, is an effective invader and is now nearly globally distributed except in the coldest areas. *Thiara* (or *Tarebia*) *granifera* (Lamarck, 1822) has been reported as an invasive species in southeastern Europe (Anistratenko et al., 2011). Several endemic species have been described from central Asia (Tajikistan, Uzbekistan). We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1 Shell whorls flattened; whorl spiral sculpture of transverse tubercle rows ..... *Tarebia granifera* (Lamarck, 1816)
[invasive in Europe and Nearctic. Oriental Bioregion, Pacific islands]

1′ Shell whorls rounded; whorls bearing sculpture ..... ***Melanoides*** **[p. 339]**

Gastropoda: Caenogastopoda: Thiaridae: *Melanoides*: Species

1 Shell moderately slender, with prominent sculpture on body whorl 2

1′ Shell very slender, upper whorls ribbed, body whorl bears with ribs weak or absent (Fig. 11.7 C) ..... *Melanoides tuberculata* (O.F. Müller, 1774)
[pantropical. North Africa. Widespread invasive]

2 Whorls flattened or virtually flat; body whorl without axial ribs (Fig. 11.7 D) ..... *Melanoides pamiricus* Lindholm, 1930
[central Asia]

2′ Whorls weakly and evenly convex; body whorl with tuberculous axial ribs (Fig. 11.7 E) ..... *Melanoides kainarensis* Starobogatov & Izzatullaev, 1980
[central Asia]

Gastropoda: Caenogastopoda: Semisulcospiridae: Genera

This key was written by D. Christopher Rogers. We caution users of these keys when identifying material in this group from regions adjacent to the Oriental Bioregion.

1	Shell elongate conic to globose; females deposit eggs on substrate; females foot, right side with an egg laying sinus 2
1′	Shell narrow to elongate conic; parthenogenic, males very rare or absent; females brood eggs and hatchlings in a dorsoposterior pouch behind the head; female foot, right side without an egg-laying sinus ..... *Semisulcospira* [Japan, Korea]
2(1)	Shell elongate conic to subovate; shell sculptured with lirae, knobs, or keels 3
2′	Shell globosely conic, unsculptured ..... *Koreoleptoxis* [Korea]
3(2)	Shell elongate conic 4
3′	Shell subovate conic ..... *Koreanomelania* [Japan, Korea]
4(3)	Apeture less than one third shell length 5
4′	Aperture approximately 50% shell length ..... *Hua* [east Asia. Oriental Bioregion]
5(4)	Operculum thin, opaque, with only a small tan central spot ..... *Namrutua ningpoensis* (Lea, 1856) [China]
5′	Operculum thick, dark brown ..... *Senckenbergia pleuroceroides* (Bavay & Dautzenberg, 1910) [China (Sichuan)]

Gastropoda: Caenogastopoda: Melanopsidae: Genera

A relatively small family with about 50 species, most of which are distributed in the southern Palaearctic region (Starobogatov, 1970; Banarescu, 1990). Three other species are endemic to the southern Pacific (Strong et al., 2008). *Melanopsis* systematics are extremely confused. All or most Palaearctic representatives have been united into a single highly polymorphic species *M. "praemorsa"* (L., 1758) with a circum-Mediterranean distribution (Glaubrecht, 1993). Other authors accept several species based on shell variation: 10 species for the Levant (Heller et al., 2005), and 15 species in the Caucausian and central Asian regions (Izzatullaev & Starobogatov, 1984; Starobogatov & Izzatullaev, 1985). Molecular analyses are needed to resolve this complicated problem.

1	Shell aperture basal margin bearing a siphonal notch or furrow 2
1	Shell aperture basal margin furrow or notch absent 3
2(1)	Shell ovoid or ovate-conic, moderately slender, smooth or prominently ribbed (Figs. 11.7 I–L) ..... *Melanopsis* [in need of revision. Mediterranean basin east to central Asia]
2′	Shell turriculate, very slender (Fig. 11.7 F) .....*Microcolpia daudebartii* (Prevost, 1821) [Asia Minor, southeast Europe]
3(1)	Shell ovate-conical with relatively large aperture; shell length <15 mm (Fig. 11.7 G) ..... *Holandriana holandrii* (C. Pfeiffer 1828) [Danube basin]
3′	Shell turriculate or high conical, length usually 15–20 mm (Fig. 11.7 H) ..... *Esperiana esperi* (A. Férussac, 1823) [Asia Minor, southeast Europe]

Gastropoda: Caenogastopoda: Lithoglyphidae: *Lithoglyphus:* Species

A small group of snails well defined conchologically by their peculiar shell appearance. This genus needs revision. Whereas Welter-Schultes (2012) accepts a single species for Europe, other authors recognize three (Anistratenko & Stadnichenko, 1994) or four (Radoman, 1983).

1	Shell subglobose, spire relatively low, SpH/AH ratio <0.50 (Fig. 11.7 A) ..... *Lithoglyphus naticoides* (C. Pfeiffer, 1828) [central and eastern Europe]
1′	Shell ovate conical, with low but prominent spire (Fig. 11.7 B) ..... *Lithoglyphus pyramidatus* Mőllendorff, 1873 [southeastern Europe]

Gastropoda: Caenogastopoda: Bithyniidae: Genera

1 Shell surface sculpture represented by thin radial striae, spiral sculptural elements absent; shell proportions not sexually dimorphic ... 2

1′ Shell spiral sculpture more or less prominent striae or riblets; male shells more slender than females ... 3

2(1) Penis complex, with flagellum and/or appendix ... ***Bithynia*** [Europe, Near East, western Siberia]

2′ Penis simple, without flagellum and/or appendix (Figs. 11.6 E, F) ... *Pseudobithynia* [southern Europe, Near East]

3(1) Shell aperture with rounded margins, without angles ... 4

3′ Aperture with two distinct angles in its upper and lower parts (Fig. 11.6 P) ... *Digoniostoma* [Tajikistan, Eastern Asia]

4(3) Shell conical with relatively high spire (Figs. 11.6 Q, R) ... ***Boreoelona*** [Siberia, central Asia]

4′ Shell globose to low conical (Figs. 11.6 S, T) ... ***Alocinma*** [Near East]

Gastropoda: Caenogastopoda: Bithyniidae: *Bithynia:* Species

This key is of limited use in the Middle East, where the taxonomy is poorly defined.

1 Whorls strongly convex (sometimes stepped), suture deep ... 2

1′ Whorls flattened or weakly convex (never stepped), suture relatively shallow ... 5

2(1) Shell height <7.0 mm ... 3

2′ Shell height typically 8–11 mm (Fig. 11.6 G) ... *Bithynia troschelii* (Paasch, 1842) [Europe, Siberia]

3(2) Penis short, compact; Balkans ... 4

3′ Penis more or less oblong (Fig. 11.6 H) ... *Bithynia leachii* (Sheppard, 1823) [Europe (except southern parts)]

4(3) Penial appendix very long, subequal to penis length (Fig. 11.6 J) ... *Bithynia kastorias* Glőer, Albrecht & Wilke, 2007 [Greece (Kastorias Lake)]

4′ Penial appendix wide and blunt, 2–3 times shorter than penis (Fig. 11.6 K) ... *Bithynia prespensis* Hadžišče, 1963 [Prespa Lake]

5(1) Shell height 8–12 mm ... 6

5′ Shell height ≤6.0 mm ... 7

6(5) Shell ovate conical; whorls flattened or weakly convex (Fig. 11.6 L) ... *Bithynia tentaculata* (Linnaeus, 1758) [widespread]

6′ Shell globose to low conical or ovoid; whorls moderately convex and evenly rounded (Fig. 11.6 M) ... *Bithynia mostarensis* Möllendorff, 1873 [Balkans]

7(5) Shell high conical, close to turriculate; umbilicus closed (Fig. 11.6 N) ... *Bithynia zeta* Glöer & Pešić, 2007 [Skasdar Lake]

7′ Shell ovate conical; umbilicus open (Fig. 11.6 O) ... *Bithynia hellenica* Kobelt, 1892 [Greece]

Gastropoda: Caenogastopoda: Bithyniidae: *Boreoelona:* Species

1 Whorls stepped, umbilicus open (Fig. 11.6 Q) ... *Boreoelona sibirica* (Westerlund, 1886)

1′ Whorls strongly convex but not stepped; umbilicus fully or partially closed (Fig. 11.3 R) ... *Boreoelona contortrix* (Lindholm, 1909)

Gastropoda: Caenogastopoda: Bithyniidae: *Alocinma:* Species

1 Shell almost globose (Fig. 11.6 S) ..... *Alocinma caspica* (Westerlund, 1902) [Caspian Sea region]

1′ Shell ovate conical or almost ovoid (Fig. 11.6 T) ..... *Alocinma sistanica* (Annandale et Prashad, 1919) [Near East]

Gastropoda: Heterobranchia: Valvatidae: Genera

About 70 species of minute, branchiate snails distributed nearly exclusively in the northern hemisphere (Starobogatov, 1970; Strong et al., 2008). Two conchologically distinct groups (sometimes ranked as subfamilies) are present in the Palaearctic: Valvatinae s. str. and Borystheniinae Starobogatov in Sitnikova, 1983. Some endemic taxa live in Lake Baikal.

1 Shell not as below, if planispiral or subplanispral then width is much less than 7 mm 2

1′ Shell with very low spire (subplanispiral), relatively large, width 7−15 mm (Fig. 11.8 A) ..... *Megalovalvata* [Lake Baikal]

2 Shell rounded or subglobose, surface smooth and glossy, sutures shallow (Fig. 11.8 B) ..... *Borysthenia naticina* (Menke, 1845) [central and eastern Europe]

2′ Shell not as above, if rounded then surface with dense, more or less prominent striae or riblets; suture deep ..... ***Valvata*** [Holarctic]

Gastropoda: Heterobranchia: Valvatidae: *Valvata*: species

1 Shell planispiral 2

1′ Shell turbospiral 3

2(1) Shell surface covered with thin radial riblets (Fig. 11.8 C) ..... *Valvata* (*Sibirovalvata*) *sibirica* Middendorff, 1851 [Mongolia, northern Europe, Russia]

2′ Shell surface smoothed, without prominent radial riblets (Fig. 11.8 D) ..... *Valvata* (*Valvata*) *cristata* (O.F. Müller, 1774) [Europe, western Siberia]

3(1) Shell surface radially ribbed or keeled, ribs prominent, uniformly separated 4

3′ Shell surface usually covered with thin radial striae, not keeled or prominently ribbed (ribs may sometimes develop around umbilicus) 9

4(3) Shell with four keels situated between upper and lower shell surfaces 5

4′ Shell ribbed but not keeled 6

5(4) Shell small, width <4 mm (Fig. 11.8 E) ..... *Valvata* (*Tropidina*) *relicta* (Poliński, 1929) [Ohrid Lake]

5′ Shell larger, width 9−10 mm (Fig. 11.8 F) ..... *Valvata* (*Cincinna*) *klemmi* Schütt, 1962 [Greece]

6(4) From Siberia 7

6′ From Ohrid Lake (Fig. 11.8 G) ..... *Valvata* (*Costovalvata*) *rhabdota* Sturany, 1894

7(6) Spire elevated, SW/SH ratio ≈0.80−1.0. 8

7′ Shell with relatively low spire. SH/SW ratio less than 0.80 (Fig. 11.8 H) ..... *Valvata* (*Sibirovalvata*) *brevicula* (Kozhov, 1936) [eastern Siberia, Mongolia]

8(7) Shell rounded (sometimes almost globose), spire whorls evenly and moderately convex (Fig. 11.8 I) ..... *Valvata* (*Sibirovalvata*) *aliena* Westerlund, 1877

8′ Shell low conical, spire whorls strongly convex (Fig. 11.8 J) ..... *Valvata* (*Sibirovalvata*) *confusa* Westerlund, 1897

9(3) Shell small, width 3.0−3.5 mm or less 10

9′ Shell larger, width typically exceeds 3.5 mm 11

10(9) Shell turriculate, up to 4.5 whorls; SH/SW ratio >1.0 (Fig. 11.8 K) ..... *Valvata* (*Cincinna*) *geyeri* (Menzel, 1904) [central and eastern Europe]

10′ Shell low conic, ≤ 4.0. whorls; SH/SW ratio <0.90 (Fig. 11.8 L) ..... *Valvata* (*Cincinna*) *saulcyi* Bourguignat, 1853 [Sicily, Near East]

11(9) Spire more or less elevated; body whorl moderately or weakly enlarged; shells with low spire; umbilicus medium-sized or narrow, 1/5 of shell diameter or less 12

11′ Spire very low, body whorl greatly enlarged; umbilicus wide, 1/3−1/4 of shell diameter (Fig. 11.8 M) ..... *Valvata* (*Atropidina*) *macrostoma* Mörch, 1864 [Europe]

12(11) Shell low conical or rounded, spire relatively low. SH/SW ratio no exceeds 1.0 13

12′ Shell ovate-conic; spire prominently elevated; SH/SW ratio 1.20−1.30 (Fig. 11.8 N) ..... *Valvata* (*Cincinna*) *antiqua* (Morris in Sowerby, 1838) [Europe, Mongolia, western Siberia]

13(12) More than two whorls raised above body whorl; shell ovate-conic or globose, if low conic then SH/SW ratio >0.85 14

13′ Shell low conic; 1−2 whorls raised above body whorl; shell relatively wide, SH/SW ratio 0.62−0.82 (Fig. 11.8 O) ..... *Valvata* (*Cincinna*) *studeri* Boeters & Falkner, 1998 [central and eastern Europe]

14(13) Shell width usually slightly less than shell height, SH/SW ratio 1.00−1.20 or greater 15

14′ Shell width subequal to or slightly exceeds shell height, SH/SW ratio 0.85−1.00 (Fig. 11.8 P) ..... *Valvata* (*Cincinna*) *ambigua* (Westerlund, 1873) [Europe, Siberia]

15(14) Shell ovate-conic with evenly rounded whorls; SH/SW ∼1.00; thin prominent radial striae (sometimes minute riblets) (Fig. 11.8 Q) ..... *Valvata* (*Cincinna*) *discors* (Westerlund, 1886) [Europe, Siberia]

15′ Whorls more or less strongly convex (not evenly rounded); radial sculpture weakly developed; SH/SW ratio 1.00−1.20 (Fig. 11.8 R) ..... *Valvata* (*Cincinna*) *piscinalis* (O.F. Müller, 1774) [Palaearctic. Invasive in North America]

..... *Valvata stenotrema* Poliński, 1929 [Lake Ohrid]

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Class Bivalvia

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INTRODUCTION

All Palaearctic freshwater bivalves belong to the orders Unionoida and Cardiida. In terms of diversity, the most important group is the superfamily Unionoidea (Unionoida), the freshwater mussels or naiads. The other three superfamilies, Cardioidea, Cyrenoidea, and Dreissenoidea (in the Cardiida), include important species like the invasive zebra mussel (*Dreissena polymorpha*) and Asiatic clam (*Corbicula fluminea*), as well as the cosmopolitan genus *Pisidium*. All freshwater bivalves are filter and/or suspension feeders, albeit some are partially pedal feeders. Although they are generally sessile, sphaeriids and unionoids may creep through the substrate. They live buried in the substratum, although the zebra mussels adhere to the substratum by a byssus or "beard".

About 45 Palaearctic Cardiida species (Bogan, 2008) and between 60 and 100 Unionoida species (Graf, 2007; Graf & Cummings, 2007; Bogan, 2008) are recognized. The Palaearctic Unionoida are not very diverse compared with other areas of the world. The classification here follows the most recently published literature (Carter et al., 2011), and the characters used have been selected from Moore (1969), Haas (1969), Ellis (1978), Piechocki (1989), Killeen, Aldridge & Oliver (2004), Kondo (2008), Jing & Zimin (2013), The MusselProject and the Mollusc collection of the Museo Nacional de Ciencias Naturales (Madrid, Spain) (Bragado et al., 2014).

LIMITATIONS

These keys are only useful for Palaearctic freshwater bivalves of the Unionida and Cardiida, both in the infraclass Heteroconchia and subclass Autobranchia. Brackish taxa such as *Batissa* (Cyrenidae) and *Potamocorbula* (Corbulidae, Myoidea, Pholadida) are excluded.

The Unionoida shell form may vary morphologically according to biotype and environmental influences, which makes identification difficult. Mussels from smaller rivers are generally less inflated than those from larger rivers, and females tend to be more inflated than males. Lake-dwelling river mussels tend to have a shortened and/or thickened anterior end. The mussels which live in hard substrates (sand, gravel, small stones) have shorter and rounder shells than those from deep, yielding sand or mud. In most cases it is the oldest part of the shell, near the umbo, which shows the original form. The remaining part of the shell is much changed during its growth.

The periostracum is paler in those forms which live under sand and small stones, but darker and duller in muddy environments. Shell sculpture, in the form of knobs or raised lines is found most often on mussels from larger rivers or in lakes. The same species can be found smooth and unsculptured in small brooks, or rough and sculptured in lakes and larger rivers.

Following Haas' (1969) classic book on the Unionoidea, the following keys are purely artificial because it is impossible to summarize the generic peculiarities of all Palaearctic freshwater bivalves. While it is possible to clearly extract distinguishing features for the orders, superfamilies, and families, it is not possible for the genera and species. Unionid shell plasticity under different environmental conditions causes some genera and species to present superficially identical forms. Molecular tools have demonstrated that isolated populations with the same phenotype may be different taxa. This makes specific determination more difficult. Sometimes, the identity of taxa can often be deduced only by distribution.

There are many species of freshwater mussels protected under law, so be certain that all necessary permits are obtained before collecting.

TERMINOLOGY AND MORPHOLOGY

The shell is divided into two **valves**, which are covered externally by the **periostracum**, a thin layer of dark, flexible, horny material. The two valves are connected dorsally by an elastic **ligament** that forms the **hinge** line. The shell edge where this ligament is found is the dorsal margin, being the opposite of the ventral margin. In Unionoida, the shorter part of the valves indicates the anterior part of the shell, while in Cyrenoida it is the posterior.

The two humps which project over the dorsal margin are the umbos. These are usually more strongly tumid than the rest of the shell. Their points typically are directed posteriorly, and on the majority of Unionoida, carry a raised pattern or sculpture of folds and/or bumps. The **umbos** are **prosogyrate** (or **prosogyrous**) if they curve in such a manner that the beaks point in an anterior direction, and **opysthogyrate** if they point in a posterior direction. In Unionoida, a small hollow, which lies posteriorly between the **umbos**, is the **lunula** or **sinulus**. A similar hollow at the posterior end of the ligament is called the **sinus** or

escutcheon. The ligament begins between the umbos and ends at the sinus. The upper part of the shell posterior end is usually more strongly compressed than the remainder of the shell, or even sulcate; it is known as the posterior slope. This is separated from the ventral part of the shell by a prominent line, which is sometimes doubled. This line runs from the umbo to the posterior point of the shell, where the dorsal and posterior margins meet. This line is the **posterior ridge**. A similar structure to this, but smaller and less clearly defined, is found on the anterior end, and called the **areola**. The remaining, far larger and curved part of the shell surface is called the **disk**. The posterior and anterior slopes can project out and exhibit *alaform* (wing-shaped) structures (**symphynotic**). These may cover the ligament. These symphynotic wings are very fragile and are often broken off on adult mussels.

The shell surface is either smooth and with growth lines, or bears raised patterns in the form of **nodes**, **nodules**, or even **spines**, which are mostly arranged in a fixed pattern. This shell sculpture can cover some or all of the shell surface. It is commonly a continuation of the umbonal sculpture, although it can also be independent. In extreme cases, only the posterior slope carries a sculpture.

The freshwater bivalve hinge is extremely variable, with internal main or **cardinal teeth** (occasionally known **pseudocardinals**) and side or lateral teeth all projecting on the broadened part of the dorsal margin called the **hinge plate**. The cardinals lie under, or in front of, the umbos, while the laterals lie at both sides of the umbo (Cyrenoidea) or are posterior (Unionoidea). The typical Unionoid hinge exhibits one cardinal and one lateral tooth in the right valve, and two cardinal and two lateral teeth in the left valve. Secondary auxiliary teeth and division of the cardinals into more teeth can occur.

The long space between the cardinals and laterals is the interval or **interdentum**. If the cardinal tooth is very thin, a shelly support, the fulcrum, may be present. While the lateral teeth can be partially or entirely suppressed, the cardinals are much more consistently structured.

In some Unionids the hinge is toothless, or provided with lamellae, similar to laterals; these do not occur on a hinge plate, but directly on the shell, in the area of the dorsal margin and are thus analogous, not homologus, with the laterals of the Unionid hinge type. These lamellae are known as **claustra**. In a few cases, knobbed projections develop under the umbo, which, like the claustra, occur directly on the shell dorsal margin. The claustra are entirely absent when these are present. The other hinge type, typical of genera *Pseudodon* and *Leguminaia*, consists of short, roundish projections on the shell dorsal margin, near or under the umbo, without a fulcrum or hinge plate. In Cyrenidae and Sphaeriidae, the hinge always has central cardinal teeth and anterior and posterior lateral teeth in each valve. The typical sphaeriid hinge is thin and shows the following structure: left valve: two cardinals (C2, C4), one anteriolateral (A2), and one posteriolateral (P2); and right valve: one cardinal (C3), two anteriolaterals (A1, A3), and two posteriolaterals (P1, P3). In *Corbicula* the hinge is strong, with three cardinals in each valve, and serrated laterals: two anterior and two posterior in the right valve and one anterior and one posterior in the left valve. The hinge in Dreissenidae is edentulous.

The mantle margin is the flesh layer that projects along the inner margin of each valve. The mantle marginal of the two valves fuse to form the **mantle isthmus** along the hinge line. If the mantle isthmus is posterior to the umbos the ligament is **opisthodetic**, but a symmetrical condition of the isthmus between the umbos gives an **amphidetic** ligament.

The valves are closed by the action of the adductor muscles, attached to the inner face of each valve. All freshwater bivalves have two adductor muscles (**dimyarian**), and if the two muscles do not differ in size they are **isomyarian** or **homomyarian**. Other muscle scars are the foot retractors and protractors and the pallial line, made by the mantle muscle. Mainly this line runs straight (**integripalleate**) or has a short hollow or sinus (**sinopalleate**).

MATERIAL PREPARATION AND PRESERVATION

Preservation technique depends on the future use (e.g., anatomy, molecular, histology). Ethanol is the best preservative for soft parts, but formaldehyde should be used for histology and anatomical studies after the specimen has been washed in water.

To examine the hinge characters, it is recommended to boil sphaeriid clams in order to open the valves before final preservation. To evaluate shell character variability, it is recommended that species accounts are studied, and the use of a binocular microscope is essential.

KEYS TO BIVALVIA

Bivalvia: Orders

1 Shell inequilateral, equivalved or subequivalved, compressed to globular; outline from circular to elongate but commonly ovate, elliptical, trigonal or trapeziform; adult size from 20 to 300 mm; umbos prosogyrous; ligament external, opisthodetic; lunule and escutheon absent or feebly defined; shell ornament from growth lines to ribs, knobs, or spines; shell nacreous, integripalliate, isomyarian or subisomyarian; anterior foot retractor forming conspicuous circular or reniform scar above and behind anterior adductor; dentition variable, some species edentolous; when present, normally two cardinals and two elongated laterals in left valve and one cardinal and one elongated lateral in right valve ..... Unionida, one superfamily: **Unionoidea [p. 348]**

1′ Shell small to moderately large; adult size from 2 to 50 mm; equivalve, isomyarian; outline circular, triangular, ovate or mytiliform; umbos anterior, central or terminal (Dreissenoidea); sculpture, when present, radial or concentric; dentition with cardinals and laterals, only cardinals or edentulous; posterior laterals, when present, lie entirely behind ligament ..... **Cardiida [p. 353]**

Bivalvia: Unionoidea: Families

1 Shell usually compressed, with shallow beak cavities; umbonal sculpture, if present, comprising two angular unjoined hooks; marsupium in the four gills; absence of diaphragm between inhalant and exhalant siphons; no water tubes in gills, which are partly free posteriorly ..... Margaritiferidae, one genus: *Margaritifera*
[in need of revision: Europe, China, Japan, Morocco, Russia, Syria. Nearctic. Oriental]

1′ Shell rounded, ovate, elliptical, trigonal or trapeziform; umbos generally sculptured; beak cavities deep; marsupium normally in two gills, sometimes in four; diaphragm between the two siphons; gills with water tubes ..... **Unionidae [p. 348]**

Bivalvia: Unionoidea: Unionidae: Genera

1 Hinge complete with up to two cardinal and two lateral teeth in left valve and one cardinal and one lateral in right valve 2

1′ Hinge teeth incomplete or absent 3

2(1) Shell surface smooth although with annuli. Sometimes with sculpture in the umbonal area and sometimes extending to the rest of the shell (species of *Acuticosta* and *Hyriopsis*) 4

2′ Shell surface strongly sculptured in the middle or lateral areas 5

3(1) Hinge toothless 16

3′ Presence of cardinal and lateral teeth or claustra 20

4(2) Hinge strong, cardinals pyramidal, serrated or notched 6

4′ Hinge thin or less developed; cardinals laminar, not massive 7

5(2) Shape rounded or oval elongated 12

5′ Shell very long and narrow, extremely inequilateral, sword-shaped, even posteriorly twisted, robust; umbo low, lying roughly 1/5 along shell length; sculpture of radial rows of nodules, which unite posteriorly with intersecting ridges, running vertically to the longitudinal axis (in some cases this sculpture covers the entire shell but usually only on the oldest parts of the valves); hinge normal, cardinals blunt, furrowed dorsally, smooth ventrally; laterals long, thick and straight (Figs. 11.17 and 18) ..... *Lanceolaria*



FIGURE 11.17 External views of the shells of *Lanceolaria*, which is found in east Russia, China, Japan, Korea, and Vietnam.



FIGURE 11.18 Inner views of the shells of *Lanceolaria*.

6(4)	Shell triangular, rounded or elongated	8
6′	Shell elongated into pointed projections at both ends, thick-shelled, twisted; posterior slope distinct, beaks low; cardinals triangular and serrated, lateral almost straight	*Arconaia*
7(4)	Shell rounded or elongated, not dorsally winged	9
7′	Shell large, inequilateral, rhomboid to irregular elliptoid, winged dorsally, compressed, rather fragile to moderately robust; posteriorly normally angularly truncated and often drawn out into a rostrum; umbo low, not or only moderately distended; sculpture of concentric, wavy wrinkles, the innermost of which are creased into a rough "W" shape, and having nodules on the creases, the outermost becoming broader and more parallel to the growth rings; the posterior slope often shows folds; color greenish to brownish, often with traces of rays; teeth in the left valve stand at an angle to the interdentum, with age, these teeth split up, the auxiliary teeth can almost reach their size, so that older mussels can appear to have 2–3 cardinals in the right, and 3–4 in the left; laterals long, a little curved, vertically hatched on older specimens, sometimes with a ventral auxiliary tooth in the right valve; interdentum narrow, curved; anterior end of the shell noticeably thicker than the posterior (Figs. 11.19 and 20)	*Hyriopsis*
8(6)	Shell heavy, elongate triangular; posterior end acute; commonly twisted on axis; umbos ornamented by radiating lines; lateral teeth striated, very long	*Cuneopsis*
8′	Shell rounded rhomboid or oval, moderately heavy, round and short in front; umbos full, with sculpture of almost parallel double "W" folds (Figs. 11.21 and 22)	*Potomida*



FIGURE 11.19 External view of the shell of *Hyriopsis*. Some species of this bivalve genus are used for pearl culture in Thailand.



FIGURE 11.20 Internal view of the shell of the mussel *Hyriopsis*.



FIGURE 11.21 External views of the shell of *Potomida littoralis* (Cuvier, 1798), a western Palaearctic species living in Spain, France, and north Africa.

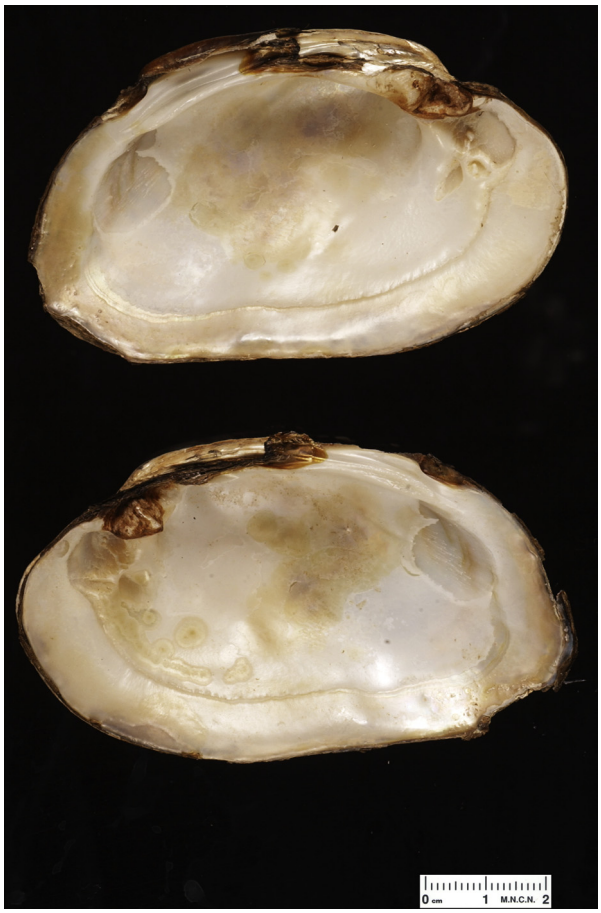


FIGURE 11.22 Internal views of the shell of *Potomida littoralis*.

9(7) Shell rounded 10

9′ Shell elongated 11

10(9) Shell strong, roundish oval, inflated, slightly inequilateral, slightly drawn out posteriorly, with strongly projecting umbones, sculptured with zigzagging, folded, concentric wrinkles; some swellings of this sculpture stretch onto the gonial ridge and onto the disk, which is formed here and there and is tuberous; gonial ridge mostly tuberous or carinate, on older examples disappearing toward the dorsal posterior; cardinals strong, compressed, serrated or notched on top; laterals short, strong and granular; interdentum inclining posteriorly; fulcrum rather prominent; umbonal cavities deep ..... *Acuticosta* [China]

10′ Shell thin to moderately robust, from roundish to almost rectangular, small to medium-sized, lake forms exceedingly robust; short and rounded in front; umbo not projecting very much, slightly swollen, with a zigzag sculpture, which can be nodular, and on some species stretch over entire shell; hinge thin and sharp or coarse and robust, but always low; umbonal cavities mostly deep; nacre whitish to dark violet; cardinals long and thin ..... *Caelatura* [north Africa]

11(9) Shell elongated, oviform or elliptoid, inequilateral, anterior rounded, posterior more or less cut off or tapered and rounded, with a long rostrum, robust, moderately distended; posterior slope prominent, slightly compressed, usually with a prominent gonial ridge crossed by curved, parallel folds, which sometimes encroach onto the otherwise smooth disk; umbo low, with umbonal cavities rather shallow; hinge normal, right cardinal blunt, low, more or less elongated; left cardinals low, short, roughened, a channel between them; in place of the interdentum there is a space; laterals moderately long, broad, pitted, right lateral sometimes having a weak auxilliary lamella ..... *Ptychorhynchus*

11′ Shell elongated, sometimes rounded, inequilateral; posterior slope more or less clearly developed; umbonal sculpture of "v"-formed hooks, wrinkles or points; cardinal teeth always laminar, sometimes serrated; shell surface mostly smooth, periostracum with or without rays (Figs. 11.23 and 24) ..... *Unio*/*Nodularia*

12(5) Sculpture of knobs, nodules or rippled (vanishing in adults in *Pronodularia*) 13



FIGURE 11.23 External views of the shell of *Unio elongatulus* C. Pfeiffer, 1825, a European species confined to some Mediterranean countries.



FIGURE 11.24 Internal views of the shell of *Unio elongatulus*.

12′	Sculpture of swollen, strong concentric furrows. Shell heavy, triangular, inflated, umbos high and central; periostracum lustrous, greenish yellow; fulcrum very strong and wide ..... *Shistodesmus*
13(12)	Hinge normal 14
13′	Reversed hinge with one cardinal and two laterals in the right shell and two cardinals and one lateral in the left; shell roundish or elongated elliptoid, inequilateral, rather robust; disk sometimes smooth without sculpture ..... *Inversidens*
14(13)	Shell very robust and solid, roundish, triangular or elliptical; inequilateral; hinge strong 15
14′	Shell not so solid, flat and rounded elliptical; more central umbos; cardinal teeth weaker than in *Inversunio* ..... *Pronodularia*
15(14)	Shell solid, oval or elliptical; hinge strong but not so robust as in *Lamprotula*; umbo reduced ..... *Inversiunio*
15′	Shell very inequilateral, roundish to roughly quadrate or even triangular, very robust, swollen; umbos high, very reduced, their sculpture consisting of a few coarse, almost parallel folds, arranged in double coils; disk usually covered in nodes or bumps; periostracum lustrous, dark or light gray, usually a little silky; hinge massive, very robust, all teeth vertically rifled or striped; dorsally situated auxiliary present in right valve ..... *Lamprotula*
16(3)	Rounded, oval, even elongated 17
16′	Very elongated, soleniform, falcate, rather thin, anteriorly narrower and rounded, ventral margin gaping anteriorly and posteriorly; posterior slope pointed at the end, ventrally and posteriorly; gonial ridge prominent; umbo low, sculpture of doubled, waved, concentric wrinkles; periostracum without rays; traces only of laterals; pallial line with a pronounced inward curve ..... *Solenaia*
17(16)	Shell inflated, umbos more central; shape extremely variable; the three following genera are very difficult to distinguish 18
17′	Shell low, elongated, compressed, thin, short and rounded in front, long and bluntly pointed behind with ventral margin gently curved, expanded posteriorly; dorsal margin almost straight, ascending posteriorly in an incipient posterior wing; sculpture of 3–5 ridges, no claustra; umbo in a rear position; hinge edentulous ..... *Pseudanodonta*
18(17)	Inflated, very large 19
18′	Shell slightly elongate, much longer than high; glochidium without hooks or larval threads ..... *Anemina*

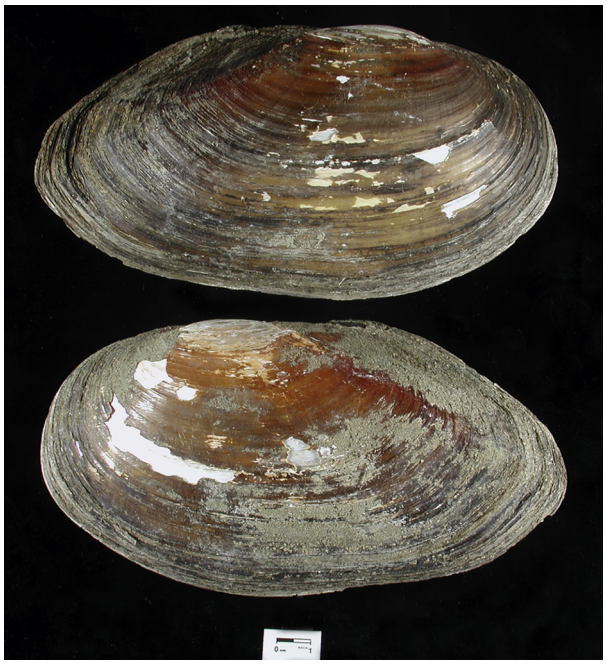


FIGURE 11.25 External views of the shell of *Anodonta cygnea* (Linnaeus, 1758), one of the larger European species of freshwater mussels in the Palaearctic.



FIGURE 11.26 Internal views of the shell of *Anodonta cygnea*.

19(18)	Shell irregularly elliptic to triangular, thin, flat to inflated, sometimes winged posteriorly; umbonal sculpture consisting of numerous, more or less parallel folds, usually doubly looped, and with nodules on the posterior part; disk smooth; periostracum shiny; glochidium with hooks; hinge reduced to thin margins of shell, curved; in lacustrine habitats with traces of claustra and symphynoty of posterior wing (Figs. 11.25 and 26) ..... *Anodonta*
19′	Very large; similar to *Anodonta* but more inflated and rounded, sometimes with circular shape (especially when young) ... *Sinanodonta*
20(3)	At least one cardinal on each valve 21
20′	No cardinals, only claustra 22
21(20)	Dorsal side of teeth covered with periostracum 23
21′	Dorsal side of teeth not covered with periostracum 24
22(20)	Shell large, thin-walled, triangular, inflated, with a high posterior slope, which is bounded by a sharp outer and a weak inner ridge; umbos very high and full, appearing tilted due to the posterior ridge; the sculpture, which stretches over the entire shell, consists of folds, parallel with the growth lines; two rows of these folds radiate from the umbo onto the shell surface—one in the middle and the other, stronger, on the posterior slope; umbonal cavities deep and wide; ligament very strong and broad, covered with concentric scales; hinge line curved with two anterior claustra in the left valve, the anteriormost is elongate, running diagonally over the hinge plate and ending sharply; posterior of it there is a weaker claustrum; further to the posterior, there are two strong claustra, the inner of which is higher, their edge is bent dorsally, and they end abruptly; right valve has a low, long anterior claustrum, and a dorsally curved posterior; nacre matte ..... *Lepidodesma*
22′	Shell usually thin, more or less elliptoid, more or less symphinote and winged posteriorly; umbos rather low, their sculpture consisting of fine, slightly looping folds, merging with coarse, low, concentric folds, parallel to growth lines; periostracum smooth, usually rayed; hinge having one long remote posterior claustrum and the trace of an anterior in each valve; the anterior may be wanting ..... *Cristaria*
23(21)	Shell generally solid, rather robust, rhomboid to elliptical, posterior ridge faint, double, ventral border curved; umbos anterior, rather full sculptured with fine, concentric ridges which tend to form two rounded loops; hinge without fulcrum, teeth arising immediately from dorsal margin of shell; single cardinal in each valve, sometimes with slight second cardinal in left valve ..... *Leguminaia*
23′	Shell higher than *Leguminaia*, ovate-rounded to elliptical, very inequilateral, posterior slope mostly high; umbos low, ornamented by "w"-shaped wrinkles; one blunt, blade-shaped cardinal in both valves, left under, right in front of the umbo; some vestiges of another cardinal or lateral teeth in some species; without a fulcrum or hinge plate..... *Pseudodon*
24(21)	Cardinal teeth compressed 25



FIGURE 11.27 External views of the shell of *Microcondylaea bonellii* (A. Férussac, 1827), a species found only in some European rivers of Italia and Croatia.

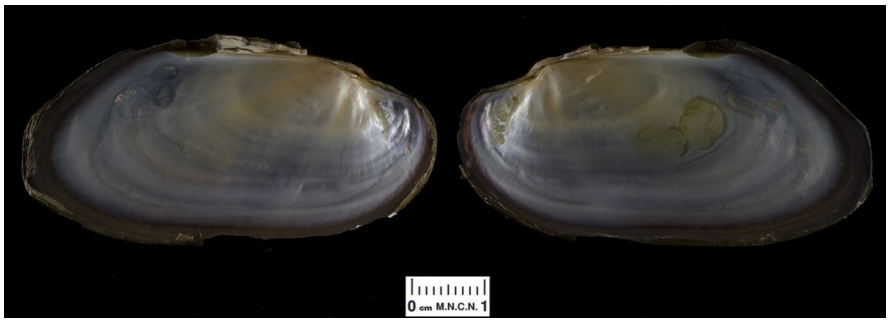


FIGURE 11.28 Internal views of the shell of *Microcondylaea bonellii*.

24′	Cardinal teeth robust; shell short oviform, swollen, robust, anteriorly rounded, posteriorly truncated, valves gaping anteriorly and posteriorly; umbonal cavities very deep; disk concentrically furrowed; periostracum brownish black, dull with indistinct rays; cardinals strong, notched, one in right valve and two in the left; two remote, indistinct laterals in left valve; interdentum very long, with exceedingly small denticles anteriorly; nacre flesh-toned, not iridescent ..... *Pseudobaphia*
25(24)	Shell inequilateral, elongate, more or less angular elliptoid, compressed, thin, with low umbos; cardinal teeth strongly stunted, compressed, single in each valve; nacre bluish or pale violet (Figs. 11.27 and 28) ..... *Microcondylaea*
25′	Shell broadly elliptoid or rhomboid, compressed, frequently weakly winged, ventral margin rounded; umbos subcentral; one cardinal in each valve ..... *Pseudodontopsis*

Bivalvia: Cardiida: Superfamilies

1	Rounded-trigonal or ovate 2
1′	Mytiliform, sometimes quadrate; hinge edentulous; umbos anterior or terminal; umbo cavity bridged by septum or myophore; bissum present; interior not nacreous; posterior adductor muscle scar long; ligament sunken Dreissenoidea, one family: **Dreissenidae [p. 353]**
2(1)	Sculpture radial, never concentric ..... Cardioidea, one family **Cardiidae** [Black and Caspian Seas]
2′	Shell smooth or with concentric sculpture, never radial; up to three cardinal teeth in either valve, pivotal cardinal in right valve ..... **Cyrenoidea [p. 354]**

Bivalvia: Cardiida: Dreissenidae: Genera

1	Mytiliform 2
1′	Shell quadrate, smooth, thick; septum with two scars, for anterior adductor and pedal retractor muscles; palial line entire ..... *Congeria*
2(1)	Anteriorly compressed; shell with a zig-zag stripes design; septum with single adductor muscle scar (Fig. 11.29) ..... *Dreissena*
2′	Septum backed by a myophore with two scars (as in *Congeria*) ..... *Mytilopsis*

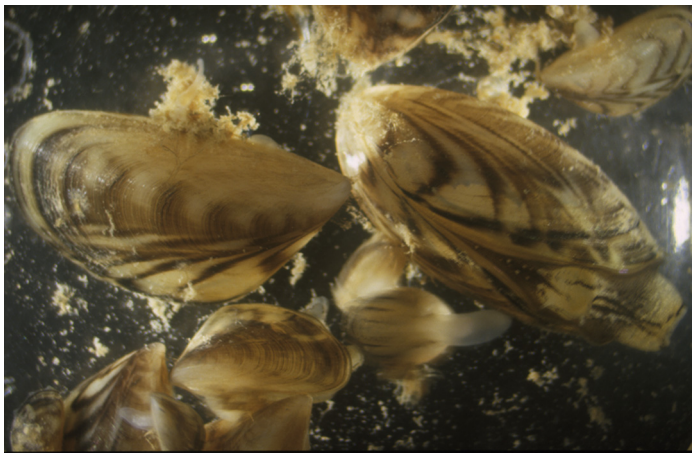


FIGURE 11.29 A cluster of the highly invasive zebra mussel *Dreissena polymorpha* (Pallas, 1771), family Dreissenidae.

Bivalvia: Cardiida: Cardiidae: Genera

1 Edentulous; valves thin, gaping at both ends; pallial sinus large ..... *Adacna* [Caspian Sea]

1′ Rounded quadrate, ribs broad; hinge with cardinals, no laterals; pallial sinus small ..... *Monodacna* [Caspian Sea]

Bivalvia: Cardiida: Cyrenoidea: Families

1 Small to moderately large; rounded-trigonal to ovate; shell solid and porcelanous with a well-developed periostracum; sculpture strong, concentric, striate; ligament external; hinge generally robust with strong posterior and anterior lateral teeth, the last somewhat serrate; pallial line entire or with small sinus ..... Cyrenidae, one genus *Corbicula*

1′ Small to minute; oval to quadrate to subtriangular; shell thin, with smooth surface (rarely with concentric ribs, which always are smaller than in Cyrenidae), sometimes with pores; ligament external or internal; hinge very narrow with anterior and posterior lateral teeth in both valves, not serrated; not more than two cardinals in each valve, always very small; right valve cardinals straight or united into inverted "v" ..... **Sphaeriidae [p. 354]**

Bivalvia: Cardiida: Cyrenoidea: Sphaeriidae: Genera

1 Shell with central umbos; animal with two siphons; shell oval, quadrate, blunty triangular in some, moderately solid, concentrically striate; hinge straight 2

1′ Shell with posterior umbos; animal with one siphon; shell small, globose or subtriangular, inequilateral; hinge curved; lateral teeth double in right valve and single in the left; two cardinals in left valve and one in the right (Figs. 11.30 and 31) ..... *Pisidium*

2(1) Umbo with a nepionic minute shell ..... *Musculium*

2′ Umbo without nepionic shell ..... *Sphaerium*

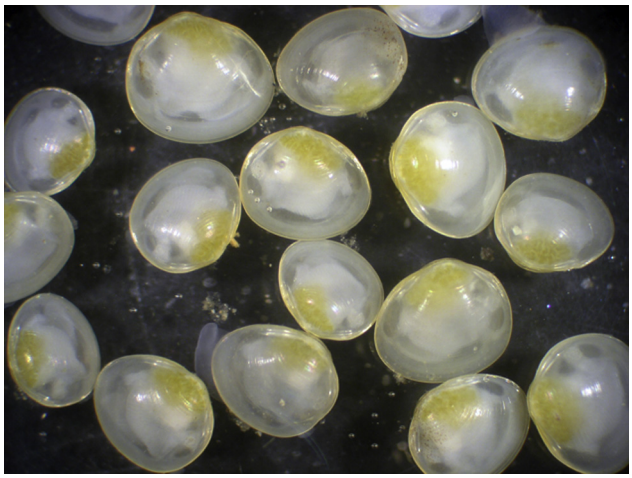


FIGURE 11.30 *Pisidium nitidum* Jenyns, 1832, is a common Holartic species of Sphaeriidae



FIGURE 11.31 The European *Pisidium amnicum* (Müller, 1774) is one of the larger species of this genus.

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Chapter 12

Phylum Annelida[1]

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[1]Citation of keys in this chapter should be made to the designated author(s) of the specific section rather than to the chapter as a whole.

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Introduction to the Phylum

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INTRODUCTION

Annelida is a diverse phylum, which contains the segmented worms. These animals live in marine, freshwater, and semiterrestrial (damp soil) habitats. Inland waters of the Palaearctic are home to many free-living aquatic worms (Oligochaeta and Aphanoneura), ectoparasitic and predaceous leeches (Hirudinida and Acanthobdellida), and ectocommensal crayfish worms (Branchiobdellida). Also present are a few species of free-living bristle worms and fan worms (Polychaeta)—a group mostly confined to marine and estuarine waters—and one species of the globally monogenetic Acanthobdellida, which are exclusively external parasites of salmonid fishes.

Traditionally, the Polychaeta, Aphanoneura, and Clitellata are considered as classes, with Oligochaeta (Fig. 12.1), Acanthobdellida, Branchiobdellida, and Hirudinea as subclasses within the Clitellata. Recent studies have shown that Polychaeta and Oligochaeta are paraphyletic groups, implying that Oligochaeta are nested in Polychaeta, rendering the latter synonymous to Annelida (see Weigert & Bleidorn 2016), while Oligochaeta includes branchiobdellids and hirudineans, so that Clitellata has become synonymous with Oligochaeta (Timm & Martin 2015). In this chapter, we keep the traditional classification of Annelida for the sake of convenience (see WoRMS, 2004), pending ongoing initiatives (Martin, pers. comm.) resulting in a new classification that takes into account the most recent advances in annelid phylogeny.

LIMITATIONS

The initial steps in separating subphyla and classes of Annelida by external structures are quite easy and should pose few problems if any for most users. One can usually also separate the groups at the subclass level by habitat: free-living and nonparasitic (a few Polychaeta and many Oligochaeta), presence externally on crustaceans (Branchiobdellida), parasitic on salmonids (Acanthobdellida), or either predators of invertebrates or external parasites on many fish species (Hirudinida).

TERMINOLOGY AND MORPHOLOGY

Knowledge of only five morphological terms is required at this higher level: segments, chaetae, clitellum, parapodia, and peristomium. **Segments** are body metameres. **Chaetae** are bristles which can have different shapes (Fig. 12.2), depending on the taxon. A **clitellum** (Fig. 12.3) is a modification of the epidermis which develops as an easily visible, glandular girdle partly on or behind the genital pores; it secretes a cocoon in which eggs are laid. **Parapodia** are paired, unjointed lateral appendages found in polychaete worms which are often fleshy (especially in marine polychaetes) and used for locomotion, respiration, and other functions. The **peristomium** is the first body segment of oligochaete annelids. It may be combined with the anterior segment, or **prostomium**.

MATERIAL PREPARATION AND PRESERVATION

Annelids can be preserved in 70%−80% ethyl alcohol for long periods; however, the best fixation for long-term preservation requires fixing them in 5%−10% buffered formalin solution for a few days, then transferring to 70% ethyl alcohol. Annelids can easily shrink or fragment during fixation and lose key taxonomic characters. This can be reduced by relaxing specimens in a 7% solution of $MgSO_4$ for 30 min before fixation.

Specimen preparation for molecular work requires avoiding exposure of the tissues to formalin. If molecular analysis is planned, a small piece of the specimen (preferably without key taxonomic characters) can be pulled and preserved in 95% ethyl alcohol or frozen at −80°C. The rest of the specimen (with key taxonomic characters intact)

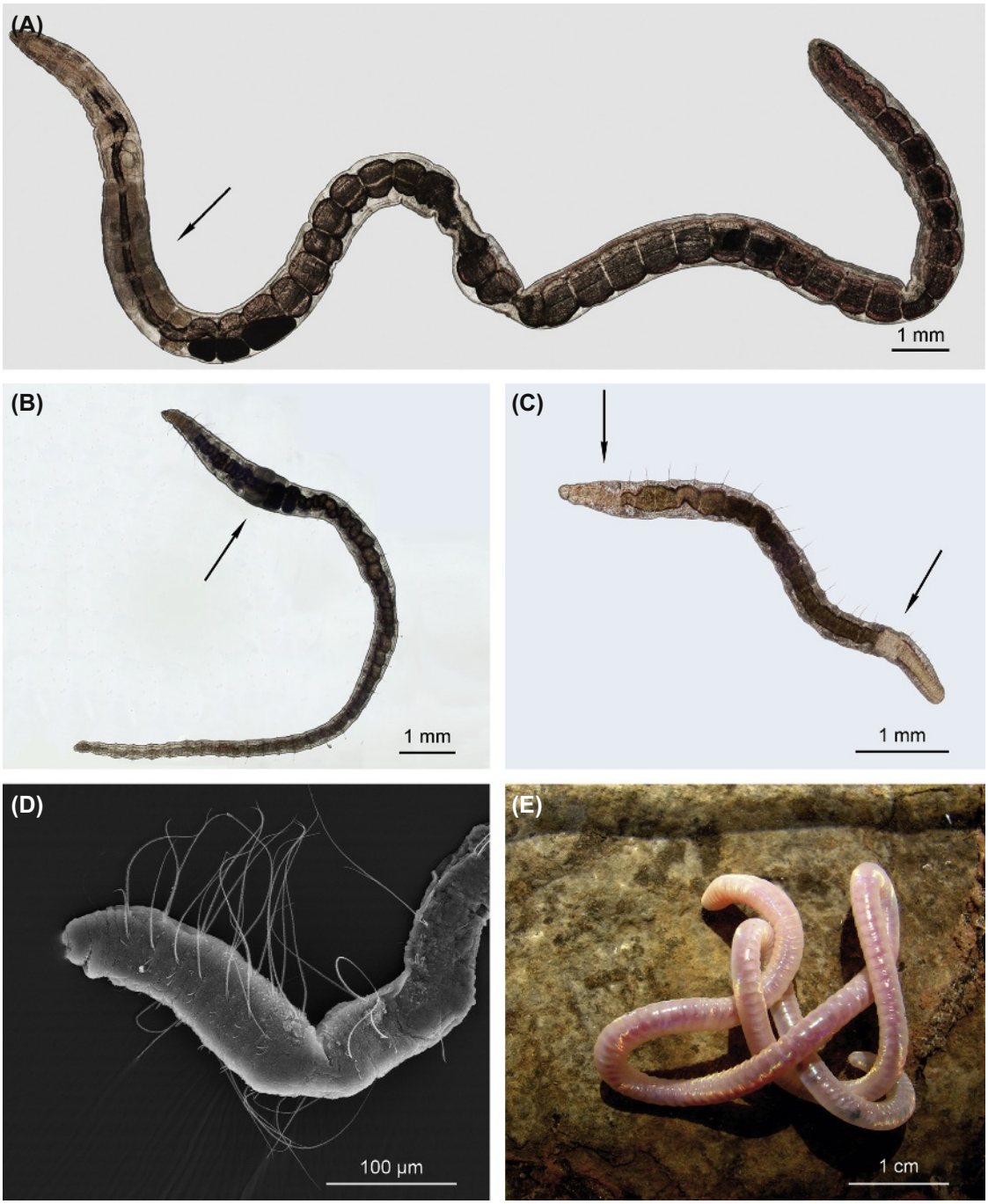


FIGURE 12.1 Examples of freshwater Oligochaeta (A–C and E: live pictures): (A) *Stylodrilus parvus* (Lumbriculidae; note the clitellum); (B) *Ilyodrilus templetoni* (Tubificidae; note the clitellum); (C) *Nais elinguis* [Naididae; note the absence of dorsal (hair) chaetae in the first segments and the budding zone in the posterior region of the body]; (D) *Parvidrilus meyssonnieri* (Parvidrilidae); and (E) *Delaya bureschi* (Haplotaxidae). *Photos A–D by Patrick Martin and E by Boris Sket.*

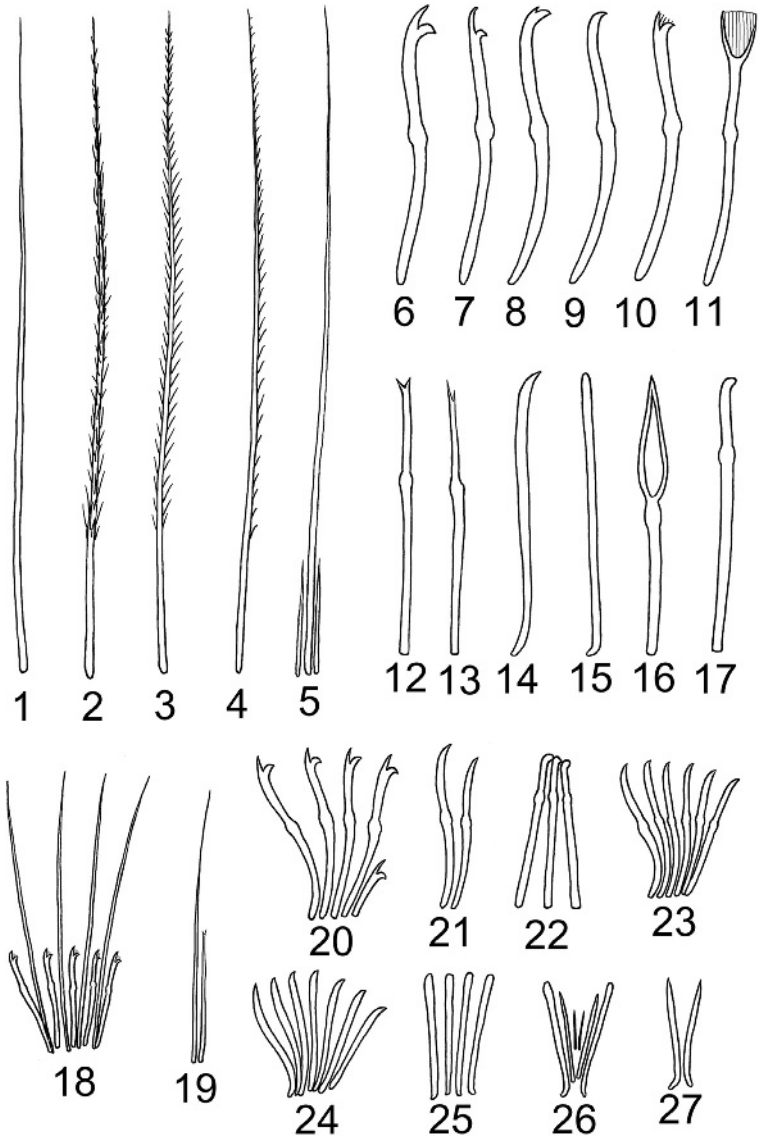


FIGURE 12.2 Types of chaetae in Oligochaeta: (1–5): hair chaetae: (1) smooth, (2) pilose, (3) plumose, (4) serrated, (5) with supporting chaetae; (6–7): short chaetae: (6) common bifid crotchet with equal teeth, (7) with shorter lower tooth; (8) with shorter upper tooth, (9) simple-pointed, (10) pectinate, (11) palmate, (12) needle chaeta with equal teeth, (13) with shorter upper tooth, (14) simple-pointed crotchet without nodulus, (15) straight chaeta, (16) furrowed spermathecal chaeta, (17) obtuse penial chaeta; (18–27) chaetal bundles: (18) dorsal bundle with hair and bifid (or pectinate) chaetae, (19) dorsal bundle with a single hair and needle chaeta, (20) bundle of bifid crotchets, (21) paired simple-pointed crotchets, (22) bundle of penial chaetae with converged distal tips, (23) *Mesenchytraeus*-type, (24) *Lumbricillus*-type, (25) *Enchytraeus*-type, (26) *Fridericia*-type, (27) paired straight chaetae.

can be fixed in formalin and preserved in ethyl alcohol as a voucher specimen for morphological use.

Due to their small size and taxonomic characters, identification and observation of annelids require a dissecting microscope with 6–50× magnification. A compound microscope with 10–1000× magnification is required for viewing whole slide mounts of small-bodied individuals or parts of specimens, such as parapodia and chaetae. For short-term examinations, use ethyl alcohol as a medium for slide mounts. When extended examination is anticipated, mounting using a 50/50 solution of glycerin and ethyl alcohol is recommended to avoid drying of the specimen. Permanent mounts for teaching or later examination can be made using commercial mounting media such as Canada balsam or Permount®.

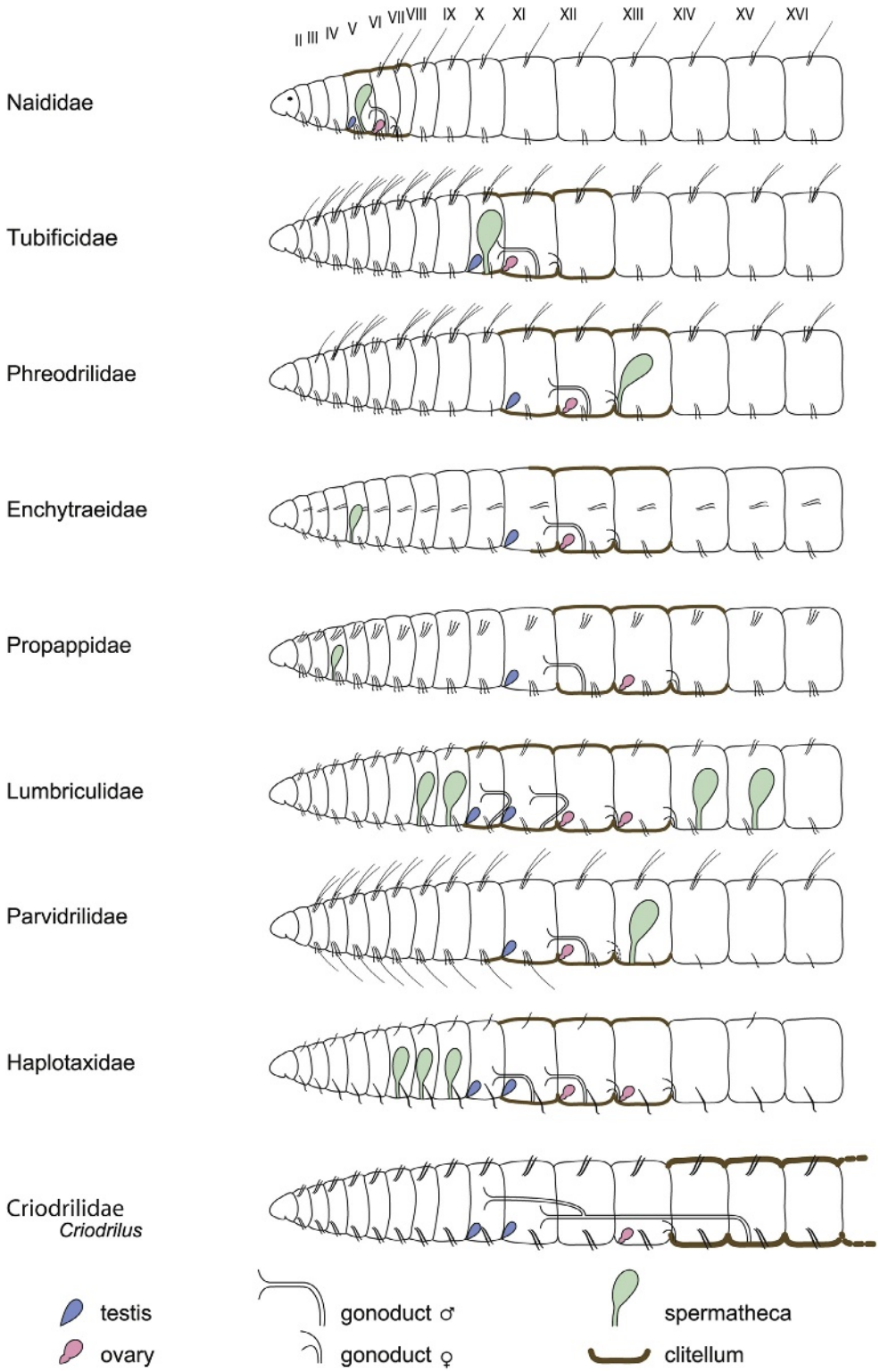


FIGURE 12.3 Location of reproductive organs in different Palaearctic families of Oligochaeta. *Redrawn after Martin and Ait Boughrous (2012).*

KEYS TO ANNELIDA

This higher classification is preliminary and a rough amalgam of the classification schemes used elsewhere (Williams et al., 2013; Timm & Martin, 2015; Verdonschot, 2015).

Annelida: Classes

1	Prostomium bearing cilia, papillae, tentacles, or scales; reproductive organs absent or associated with various structures or organs; parapodia present, reduced, or absent; chaetae relatively abundant; clitellum always absent 2
1′	Prostomium simple; reproductive organs combined with a tumid region called a clitellum; parapodia absent; chaetae relatively scarce or absent ..... **Clitellata [p. 364]**
2(1)	Minute worms, 1−2 mm or chains of zooids up to 10 mm; hair chaetae in both dorsal and ventral bundles; no eversible pharyngeal pad, prostomium with cilia used for gliding motion only; ventral copulatory glands in rare mature specimens; nervous system ladder-like (Fig. 12.1) ..... **Aphanoneura [p. 508]**
2′	Minute to large worms; prostomium with papillae, tentacles, or scales; parapodia may be present ..... **Polychaeta [p. 515]**

Annelida: Clitellata: Subclasses

1	With one (caudal) or two external suckers (caudal and cephalic); chaetae usually absent 2
1′	Without external suckers; chaetae usually present ..... **Oligochaeta [p. 369]**
2(1)	Twenty or more body segments; external annulation finer than actual segmentation 3
2′	Eleven externally obvious body segments plus four segments fused into head/pharyngeal region; posterior end with a sucker, anterior end with ventral adhesive surface; two chitinous jaws in the pharynx; chaetae always absent ..... Branchiobdellida, one family: **Branchiobdellidae [p. 487]**
3(2)	Body divided into 32 postoral segments; segments subdivided superficially into 3−16 annuli, anterior (oral) sucker present consisting of four segments: mouth on ventral surface of anterior sucker; three jaws present or absent; posterior (caudal) sucker consists of seven segments; chaetae absent from entire body; median ventral unpaired gonopores ..... **Hirudinida [p. 495]**
3′	Body divided into 29 postoral segments; segments subdivided superficially into four annuli (a1, a2, b5, b6); chaetae present anteriorly in five consecutive cephalic segments; median ventral unpaired gonopores; ectoparasitic on fish ..... **Acanthobdellida [p. 507]**

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Class Clitellata: Subclass Oligochaeta

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INTRODUCTION

The Oligochaeta as treated in this chapter is a paraphyletic subclass including the Class Clitellata except the leech-like groups Branchiobdellida, Acanthobdellida, and Hirudinea. More than 1100 species of at least 20 families live in fresh water, among them over 600 species in that of the Palaearctic Region (Martin et al., 2008).

LIMITATIONS

The traditional family Tubificidae is maintained, for convenience, in its former sense in this chapter, although being a paraphyletic stem group for the Naididae (s.s.), Pristinidae and Opistocystidae, and integrated to Naididae (s.l.) in a phylogenetic system (Erséus et al., 2008; Schmelz & Timm, 2007; Timm, 2012). Besides the typical freshwater groups of Oligochaeta, some aquatic or amphibious representatives of the mostly terrestrial orders of Crassiclitellata (earthworms) and Enchytraeida are included in the keys. The marine and brackish water forms are mostly excluded, except those also occurring near the shore, virtually freshwater lagoons and estuaries, or in the continental brackish water lakes including the Caspian Sea. Separate keys were produced for the Naididae, Tubificidae, and Lumbriculidae of Lake Baikal, as well as for all Oligochaeta known from the Caspian Sea, since the fauna of these large lakes includes many endemic species not found elsewhere (Martin, 1996).

Globally, the last survey of freshwater oligochaetes by Brinkhurst & Jamieson (1971); Brinkhurst et al. (1984) is considered to be out of date, although it is still of great use. Besides that magnus opus, several modern identification guides and catalogs exist at national and regional scales in the Palaearctic: the former USSR (Chekanovskaya, 1962), Lake Baikal (Semernoy, 2004), the northern part of Europe (Timm, 2009), Poland (Kasprzak, 1981), the former Czechoslovakia (Hrabě, 1981), groundwater of southern Europe (Giani et al., 2001), China (Wang & Cui, 2007), and Maghreb (Martin & Aït Boughrous, 2012). At the family level, the monograph on the Naididae and Pristinidae of the world by Sperber (1948) has not lost its value to date. A guide to the European freshwater Enchytraeidae was recently made available by Schmelz & Collado (2010). Other information on the surface freshwater oligochaete fauna of southern Europe, Turkey, Japan, the Russian Far East, and other countries is scattered in hundreds of separate papers but has never been properly surveyed.

There is no space for full descriptions of species in this book. Whenever possible, the keys are based on external characters (chaetae, etc.) visible on entire worms, either alive or mounted. Details of internal anatomy (particularly the structure of gonoducts and spermathecae) are included only when unavoidable. For the same reason, keys lead from families to genera or species, omitting the subfamilies and genera often separable only on the grounds of internal anatomy.

TERMINOLOGY AND MORPHOLOGY

External Anatomy

The length of freshwater oligochaetes ("L") varies usually between 1 mm and several centimeters, in preserved material (Fig. 12.1). The body is mostly soft and smooth but in some taxa is armored with **epidermal papillae** and/or secretions and adhered particles. New segments are successively formed in the posterior body end, thus the total segment number is usually variable. The first segment, or **peristomium**, surrounding the mouth, is always devoid of **chaetae**. Roman numerals are used for marking the segments and Arabian numerals for the intersegmental furrows or dissepiments—e.g., 3/4 is the furrow and dissepiment between segments III and IV. A small tactile appendage called **prostomium** is attached to peristomium above the mouth; sometimes it can be extended into an unpaired **proboscis** (tentacle). A pair of pigmented eyespots may be present on the prostomium in some Naididae. Only few oligochaetes have external **gills**.

Chaetae (called also **setae**) are present in four bundles (two ventral, and two dorsal or dorsolateral bundles) on each segment except the first and, sometimes, also the genital and some other segments, very seldom entirely lacking. There are two basic types of chaetae (Fig. 12.2). (1) Short S-shaped or sigmoid chaetae, also called **crotchets**, usually with a median thickening (**nodulus**) and with a bifid distal tip. The two teeth (or **prongs**) of the ectal end are called the upper or distal, and the lower or proximal tooth, respectively. The bifid chaetae, modified by the presence of intermediate denticles or a wavy web between the two teeth, are called **pectinate** or **comb-like** chaetae. When the intermediate and outer teeth become equally large and connected with each other, the chaetae are called "**palmate**." The teeth can be of uneven length and thickness; particularly the upper tooth tends to reduce or even disappear. Spade-like, brush-like, etc., versions of bifid chaetae can occur in some species. The short chaetae can be also simple pointed, either sigmoid or straight and bacilliform, sometimes even without a nodulus. The dorsal bifid chaetae can be modified as straight, sharp-tipped needle chaetae, either bifid or simple pointed. The ventral chaetae located at genital pores can be modified as genital chaetae (see below). (2) The second basic chaetae type is long and thin hair chaetae (or hairs), simple pointed, without any nodulus. They can be covered by fine hairs (called **hirsute** or **pilose chaetae**); these hairs or **denticles** can be distributed in one or two longitudinal rows (in **serrate or plumose hair chaetae**, respectively). Often, the hair chaetae look smooth under a light microscope, while finely pilose in photos produced by scanning electron microscopy (SEM). Usually the hair chaetae, when present, occur only in the dorsal bundles. Chaetae can be more numerous and diverse in the anterior body part, while becoming gradually more scarce and uniform in the tail portion.

The **clitellum** is a muff-like or saddle-shaped, glandular thickening of the external mucous epithelium in sexually mature Oligochaeta. It covers several segments, mostly including those with male and female genital pores. The genital pores are usually ventral and paired, located on the line of ventral chaetal bundles. The male pores are more prominent, often lying on a glandular protuberance, seldom on an external penis, usually one to two pairs, either on X–XII segments or even further forward in the smaller oligochaetes (microdriles) but on XIII–XVIII in earthworms (megadriles). Seldom there is a single median male pore. Female pores (mostly a single pair) are inconspicuous and located in intersegmental furrows either immediately after the male pores or for one segment backward (but before them in earthworms). Spermathecal pores can lie either immediately before or/and after the male and female pores, or further onward for several segments, either ventrally, laterally or dorsally, sometimes even unpaired. Spermathecal pores are often distinct, like the male pores. Penial chaetae are usually blunt-tipped; with several per bundle, their tips are often converging. The penial chaetae (and any other ventral chaetae) are usually lacking at male pores when there exist internal chitinous penial sheaths. The spermathecal chaetae are mostly sharp-tipped, with a longitudinal groove (or, maybe, a hollow optically similar to groove), and equipped with a distinct gland at their base. Modified chaetae of spermathecal type can sometimes occur both at the spermathecal and male pores. A forward shift of the whole genital system often occurs in the forms with prevailing vegetative reproduction. The latter can happen with simple fragmentation (architomy), or with paratomy (budding); in the latter case budding zones evolve in the posterior body region after a fixed number of body segments (marked with "n").

Internal Anatomy

The body cavity of each segment is usually separated from that of neighboring segments by **muscular/epithelial dissepiments (or septa)** and, in its turn, is divided into left and right parts by a mesentery. Coelomocytes of various size and structure can float freely in the coelom fluid of several oligochaete taxa.

In aquatic Oligochaeta, the digestive tract is a strict longitudinal tube consisting of five to six consecutive sections. A simple mouth cavity is followed by **pharynx** characterized by a dorsal, muscular/glandular roof called the **pharyngeal pad**. Paired **pharyngeal glands** (or **septal glands**) can reach for several segments backward. A narrow **esophagus** develops into a wider **midgut** or intestine after several segments. Sometimes the beginning of the midgut is dilated and referred to as a stomach. The midgut nearly fills the coelom cavity of most body segments, narrowing whenever piercing a dissepiment. The midgut as well as the posterior portion of esophagus are covered with a layer of darker cells, the **chloragogen tissue**. The simple hindgut occupies a few hindmost segments. Different appendages and modified portions of the wall can occur at the esophagus or the beginning of the intestine.

There are at least two large, longitudinal blood vessels, connected with each other by transverse vessels in some segments. The dorsal vessel pulsates, pumping blood forward. One or several pairs of the anterior transverse vessels can be modified into muscular, pulsating "hearts" while the posterior transverse vessels can be turned into blind appendages of the dorsal vessel. A blood sinus inside the intestinal wall is common, and in larger worms there are also different additional, smaller blood vessels. Dissolved hemoglobin gives the blood a red or pink appearance in many live oligochaetes.

The excretory system includes a number of paired metanephridia. These consist of a ciliated funnel on the anterior surface of a dissepiment (anteseptale), and of a duct piercing the dissepiment and winding in the cavity of the next segment before opening with a ventral pore (postseptale).

The central nervous system is represented by the **ventral nerve cord** with a pair of merged ganglia in every segment except the foremost ones; the **dorsal brain**; and connecting them is a **circumpharyngeal nerve ring**. The brain is usually located in segments I–III. External sensory papillae are most abundant on the prostomium (which can even form a tactile proboscis); although usually inconspicuous, the papillae can be prominent in armored species where they penetrate the armor. Pigmented eyespots on prostomium occur in some genera.

As a rule, the reproductive organs are paired (Fig. 12.3). The testes are located in segments X and XI, with the ovaries in XII and XIII, which are assumed to correspond to the plesiomorphic gonadal pattern. This number is reduced to one to two pairs of testes and one pair of ovaria in most families. Most often the single pairs of testes and ovaria are located either in their original segments XI and XII, respectively, or in X and XI. A forward shift (or, seldom, a backward shift) of the whole reproductive system occurs in some taxa.

Developing gametes are usually floating in the coelom of the gonadal segments. The posterior (or also anterior) wall (**dissepiment**) of a gonadal segment is often bulging into neighboring segment(s), then forming a (single or paired) sperm or egg sac. The posterior sperm sac is always surrounded by egg sac, the ripe eggs usually lying behind the sperm mass. These sacs can occupy many segments behind the **clitellum** and be the most conspicuous element of the reproductive system. **Gonoducts** are almost always paired. Male ducts include a ciliated sperm funnel at the posterior wall of a testicular segment, and a sperm duct or **vas deferens** piercing the dissepiment and usually winding in the coelom of the next segment. The vas deferens can open immediately as a male pore in the body wall, or into various terminal elements of the male duct, called atria and penes, or penial bulbs. The **atrium** is a spacious chamber with glandular walls. Bodies of gland cells of the atrial wall

are called **prostatic glands** when bulging into the coelom. They can either cover the outer surface of the atrium (as a diffuse prostate), or form aggregations connected with atrial lumen by a common narrow stem (**compact prostates**; not to confuse with the **homonymous prostates** of many earthworms which are separate organs located near the male pores). When the distal end of atrium is modified for protrusion during copulation, it is called **pseudopenis**. The atrium can also terminate with a true penis, surrounded by a penial sac when not protruded (seldom is the penis permanently external). Sometimes there is a narrow efferent duct (vas efferens) between the atrium and penis. The penis can be either completely soft or surrounded by a more or less chitinized penial sheath. Male pores, located near or instead of the ventral chaetal bundles of the respective segment(s), are usually the most prominent external genital organs beside clitellum.

There are three types of **male gonoduct: plesiopore** (with external pores in the segment following the testicular one, as in most aquatic oligochaetes), **prosopore** (with pores in the same segment as the testes), and **opisthopore** (with the male pore several segments behind the testes). In the case of the semiprosopore condition, the first of two pairs of vasa deferentia lack their own atria and join atria of the second pair. The prosopore vasa deferentia can either pierce twice the post-testicular dissepiment, or only cling to its anterior surface before joining the atrium. Sometimes the male pores of the left and right side can open into a common, median copulatory chamber, or there can be a single, unpaired atrium receiving all vasa deferentia. Female ducts are vestigial, consisting only of a ciliated funnel at the posterior wall of the ovarial segment, and an inconspicuous female pore in the nearby intersegmental furrow.

Spermathecae are another important element of the reproductive system. Their number and location are variable, from one single spermatheca to many pairs, and from the immediate neighborhood of the male and female pores (anteriorly or posteriorly) to many segments before them. They can be simple inversions of the body wall, or differentiated into **ampulla** and external duct; the ampulla can bear diverticula, and the duct can be covered with a glandular layer or bear separate glands. Sperm contained in the spermathecae can be amorphous or arranged into bundles or even spermatozeugmata. The spermatozeugmata consist of fertilizing and nonfertilizing spermatozoa, the latter forming a cortex around the former. They are typical of most Tubificinae but may be exceptionally present also in the Rhyacodrilinae (Tubificidae). Sometimes an internal duct connects the ampulla with the digestive tube. External pores of the spermathecae can lie either amidst a segment or in an intersegmental furrow. Spermathecae can be lacking in parthenogenetic individuals of some taxa, and also in taxa attaching external spermatophores to the partner's body surface.

MATERIAL PREPARATION AND PRESERVATION

Immature Oligochaeta are often unidentifiable; when available alive, they can be cultivated in small aquaria with natural substrate at 4−12°C until sexual maturation. This can take several months and the results are not always positive. Cultivated individuals may be more suitable for reference collections as lacking possible injuries (lacking tails and broken chaetae), common after sampling in nature.

A microscopical study of live individuals is recommended if possible; it is the prevailing method for the Enchytraeidae. Living worms are relatively transparent so that most internal organs are visible, as are their intestine peristaltics, blood vessel pulsation, and nephridial ciliary movement. The mobility of live worms can impede continuous investigation, photographing, or even measuring any structures. A slight pressure on the worm under a coverslip can be helpful, unless the animal bursts; after which only chaetae will remain well exposed. Different methods of immobilization can be used for small oligochaetes, e.g., putting them under a coverslip in a drop of carbonated water. Then the worm will stay still due to suffocation but may survive for 10 min or more.

Fixative makes the body wall opaque so that internal organs become hardly distinguishable. Fixed oligochaetes can be studied in temporary mounts under a coverslip in glycerine, which makes their bodies soft and semi-transparent. Glycerine is well soluble in water and alcohol, and temporary mounts can last several years when the coverslip edges are sealed. Type and reference specimens should be maintained in permanent whole mounts, e.g., in Canada balsam. For this, the worms can be transferred from glycerine over diluted and absolute alcohol into xylene, then put into a drop of balsam/xylene and covered with a coverslip. After some days of the slip edges desiccating, the mount is ready and can survive a hundred years, if not more. Larger oligochaetes can be fixed by being pressed flat between two slides. Internal organs have better visibility in Canada balsam when in glycerine, particularly if the worms were slightly stained in toto before mounting (the paracarmine method is probably the most widely used procedure for this purpose, including differentiation in acid 80% alcohol). Chaetae can be difficult to observe as their refractive index is close to that of balsam, particularly if a standard light microscope is used. Differential interference contrast (DIC) microscopy makes observations of chaetae and internal organs much easier to observe. There exist several other clearing media for temporary investigation, as well as synthetic resins for making permanent mounts (e.g., euparal); however, the persistence of these over time has not yet been tested.

Brinkhurst (1960) introduced, and many subsequent researchers have used, Amman's lactophenol (consisting of glycerine, water, phenol, and lactic acid) for preliminary studies, and polyvinyl lactophenol for making semi-permanent whole mounts of aquatic Oligochaeta. These media are good for routine identification by making the chaetae and other chitinous structures distinct. Unfortunately, they are unsuitable for reference material since all soft internal organs will merge in a continuous mass under a coverslip, and even chaetae will swell after some years.

A close inspection of internal reproductive organs, particularly the male ducts as is necessary for a detailed taxonomic study, is often overshadowed by amorphous masses of sperm and the prostate glands of whole mounts. For this purpose, the genital segments can be dissected: a part of the body wall is removed, the male ducts and the spermathecae extracted under a dissecting microscope, using sharp razor blades and very fine needles, or ophthalmology instruments (iris knife, see Martin & Aït Boughrous, 2012). It is risky as these organs are soft and can easily get lost. Furthermore, it is difficult to mount dissected small objects. Taxonomically valuable material is more securely maintained when histological sections are made from the segments of interest, and internal organs are reconstructed after the sections. This time-consuming procedure is not described here. A routine identification can always proceed using either live or whole mounted oligochaetes, while taxonomically puzzling specimens, if present, could be sent to an expert.

When beginning the identification of an oligochaete, first establish the anterior end which is usually thicker, bearing the mouth and prostomium, and more numerous and longer chaetae on several segments. The tail portion is usually thinner and longer, and without many taxonomic characters (if not bearing gills). Then distinguish the dorsal and ventral sides: the hair chaetae, when present, occur in the common taxa only dorsally. The prostomium also lies dorsal to the mouth; it can be extended into unpaired proboscis, or bear a pair of simple egg spots. Genital pores, if present, are almost always ventral. Count the segments (do not forget that usually the chaetae begin on II but never on segment I); the total segment number is not so important as are the presence (or absence) and position of the reproductive system elements (clitellum, genital pores, internal reproductive organs bulging the body, modified ventral chaetae). The latter is most probably located in the region of segments IX–XIII. The male pores are often prominent as tubercles in the anterior portion of clitellum, while the spermathecal pores lie often (but not always) ahead of the clitellum. The female pores are usually inconspicuous. The sperm and egg sacs can reach for several segments rearward, obvious as massive bodies above the intestine. The body wall is externally smooth in most oligochaetes but can be armored with cutaneous papillae and/or adhered particles in some. The tail portion is usually devoid of specific characters, except the forms with external gills.

Chaetae: are they of one sort or different (bifid, simple pointed, and hair chaetae)? Number of chaetae per bundle: two, one, or variable? The chaetal number and diversity are usually largest in the anteriormost (preclitellar) segments while decreasing in the tail portion. The absolute length of chaetae is usually less important than the relative length (sometimes, also thickness) of them in separate body regions. Variations of shape must be observed in the hair (smooth, pilose, serrate) as well as in the dorsal bifid (pectinate with intermediate teeth?) chaetae. In the ventral and dorsal bifid chaetae, the relative length of the upper and lower teeth is important, also the position of nodulus (proximal, medium, or distal), and the thickness of chaetae; all these characters can successively change along the body length. The segments bearing male and/or spermathecal pores can lack ventral chaetae, or they can be replaced with modified genital chaetae (penial or spermathecal, respectively) in the sexually mature, maturing, or postreproductive individuals, even in those devoid of a clitellum. The bundles of penial chaetae, as well as chitinous penial sheaths present in many taxa, are often hidden inside the body and visible only in living individuals or cleared whole mounts.

The digestive tract is the most readily apparent internal organ, traceable even in whole mounts and in immature specimens. The pharynx roof (pharyngeal pad) in segments II–III is more or less thickened, covered with gland tissue, and fastened to the dorsal body wall with numerous muscles. The relatively thin esophagus follows through several subsequent segments, dilating into midgut (intestine) usually already in one of the anteclitellar segments. Different glands, appendages, and modified parts of wall can occur at the pharynx, esophagus, and anterior portion of the midgut, particularly in the Enchytraeidae. Dark chloragogen tissue covers the digestive tract, usually beginning with a certain esophageal segment. The dorsal and ventral blood vessels are usually well distinguishable in whole mounts but usually of inferior value for identification. The number and modifications of commissural vessels in some segments (as dilated "hearts," or blind appendages, sometimes covered with chloragogen tissue) can be more important. Nephridia are visible only in living or cleared specimens; their structure and presence/absence in the anterior segments is important, especially in Enchytraeidae. Spermathecae are one of the most distinct elements of the reproductive system in whole mounts since they are usually not shadowed by clitellum. Their structure

and segmental location, position of their pores on a segment (ventral, lateral, etc.), and arrangement of sperm in the spermathecal ampulla (amorphous, in bundles, organized into spermatozeugmata?) are important. Testes, ovaria, sperm sacs, and egg sacs have few identification characters. Separate elements of the male ducts (funnels, vasa deferentia, atria, prostatic glands, penial apparatus) are most important for the oligochaete taxonomy but often hardly distinguishable in whole mounts. Different special methods like DIC microscopy can be sometimes helpful here, as well as dissection or sectioning of the gonadal segments.

It would be reasonable to maintain unidentifiable (potentially new for the region or science), sexually mature oligochaetes discovered in routine surveys, in fluid (preferably alcohol) for further study by an expert. When having live oligochaetes available, one could fix some of them (at least, their posterior portion) in strong (absolute), not denaturized alcohol for possible DNA sequencing.

KEYS TO OLIGOCHAETA

In the case of the most diverse families (Naididae, Tubificidae, and Lumbriculidae), separate keys are given for the fauna of Lake Baikal because this ancient lake is so rich in local endemic species (pp. 387, 433, and 471, respectively). For the same reason, a separate key is given to the Oligochaeta of the brackish water Caspian Sea (p. 479).

Oligochaeta: Orders

1	Hair chaetae lacking 2
1′	Hair chaeta present ..... **Tubificida** (in part) **[p. 369]**
2(1)	Chaetae sigmoid or strict, either simple pointed or with shorter upper tooth, two or more per bundle, seldom by one or completely lacking; spermathecal pores either near the male and female pores or far anterior to them 3
2′	Chaetae always sigmoid, usually bifid with nodulus, their shape and number per bundle mostly variable; spermathecal pores in the neighboring segment(s) with the male and/or female pores, most often in the testicular segment ..... **Tubificida** (in part) **[p. 369]**
3(2)	Spermathecae in the segments nearby the genital pores or further forward but then not delimited to V; chaetae always sigmoid, never more than two per bundle (paired), seldom single or lacking 4
3′	Spermathecae in V, opening in 4/5, seldom in IV, while the male pores are usually located in XII; chaetae strict or sigmoid, mostly in variable number but sometimes paired, single, or lacking ..... **Enchytraeida [p. 445]**
4(3)	Clitellum unilayered; mostly smaller worms (“microdriles”); male ducts and location of male pores variable; spermathecae immediately before or/and after the segments bearing male and female pores; chaetae simple pointed or with reduced upper tooth, mostly paired but sometimes single or lacking 5
4′	Clitellum thick, multilayered, often long, sometimes shifted backwards from the genital pores; male ducts opisthopore, male pores can lie on different segments and be distinct or inconspicuous; spermathecae often several pairs, far before the genital pores, sometimes lacking; chaetae always paired (except some Megascolecidae revealing numerous chaetae arranged in a ring round each segment), simple pointed. Relatively large worms (“megadriles” or “earthworms”) ..... **Crassiclitellata [p. 454]**
5(4)	Male ducts prosopore or semiprosopore (seldom plesiopore), almost always with atrium and often also with penis. Male pores mostly in X, or in IX and X, sometimes only in VIII or IX ..... **Lumbriculida [p. 457]**
5′	Male ducts plesiopore, very simple. Male pores in IX and X ..... Haplotaxida, one family: **Haplotaxidae [p. 478]**

Oligochaeta: Tubificida: Families

1	Hair chaetae only in the dorsal bundles, or completely lacking 2
1′	Hair chaetae present dorsally and ventrally, accompanied by single pointed needle chaetae in dorsal, and by bifid crotchets in the ventral bundles; chaetal bundles beginning always in III; very tiny worms ..... Parvidrilidae, one genus: ***Parvidrilus*** **[p. 370]**
2(1)	Vegetative reproduction by paratomy (with budding zones) prevailing, reproductive system seldom developed; male pores, if present, in V, VI, or IX, spermathecal pores in the preceding segment 3
2′	No paratomy; reproduction exclusively sexual, in rare cases alternating with architomy (simple fragmentation); male pores usually in XI or XII, seldom in VIII, IX, or X, spermathecal pores in the preceding or following segment 4
3(2)	Male pores in IX, spermathecal pores in VIII; dorsal bundles beginning in II (as an exception, in III or IV in one species), with hair chaetae ..... Pristinidae, one genus: ***Pristina*** **[p. 370]**

3′	Male pores in V or VI, spermathecal pores in IV or V, respectively; dorsal bundles beginning in VI, V, IV, or III, seldom in II or further backwards, with or without hair chaetae, seldom completely lacking ..... **Naididae [p. 373]**
4(2)	Male pores in XI (seldom in VIII, IX, or X), spermathecal pores in the preceding segment, seldom lacking; dorsal bundles beginning in II ..... **Tubificidae [p. 394]**
4′	Male pores in XII, spermathecal pores in XIII; dorsal bundles beginning in III ..... **Phreodrilidae [p. 443]**

Oligochaeta: Tubificida: Parvidrilidae: *Parvidrilus*: Species

1	Genital chaetae absent 2
1′	Modified penial chaetae present (one per bundle in XII), their enlarged, spearhead distal end with spatulate curvature. L = 1.3−1.6 mm; mine galleries ..... *Parvidrilus meyssonnieri* des Châtelliers & Martin, 2012 [France]
2(1)	Unpaired spermatheca present 3
2′	Spermathecae absent. L = 2 mm; only known from Corveissiat cave ..... *Parvidrilus jugeti* des Châtelliers & Martin, 2012 [France]
3(2)	Spermatheca in XII (atrial segment) 4
3′	Spermatheca in XIII (postatrial segment) 5
4(3)	Spermathecal ampulla tubular; atria elongate (about 150 µm long). L = 1.2 mm; only known from Sa Ucca de su Tintirriolu cave ..... *Parvidrilus tomasini* Sambugar & Martínez-Ansemil, 2012 [Italy: Sardinia]
4′	Spermathecal ampulla ovoid; atria very elongate (about 250 µm long). L = 1.2 mm; only known from Monte Maiore cave ..... *Parvidrilus stochi* Sambugar & Martínez-Ansemil, 2012 [Italy: Sardinia]
5(3)	Spermathecal ampulla regularly ovoid or round; atria elongate 6
5′	Spermathecal ampulla of irregular shape, very large; atria short, pyriform. L = 1.3−1.5 mm. ..... *Parvidrilus spelaeus* Martínez-Ansemil, Sambugar & Giani, 2002 [Italy, Slovenia]
6(5)	Spermathecal ampulla ovoid; atria elongate, about 150 µm long. L = 1.2 mm; only known from Seldesuto cave in Cantabria ..... *Parvidrilus gianii* Martínez-Ansemil & Sambugar, 2012 [Spain]
6′	Spermathecal ampulla small and round; atria tubular, somewhat curved, about 32 µm long. L = ?; only known from Estaragueña cave in Cantabria ..... *Parvidrilus camachoi* Martínez-Ansemil & Sambugar, 2012 [Spain]

Oligochaeta: Tubificida: Pristinidae: *Pristina*: Species

1	Prostomium with proboscis (tentacle) ..... (subgenus *Pristina*) 2
1′	Prostomium simple, without proboscis ..... (subgenus *Pristinella*) 9
2(1)	No extra long chaetae in III 3
2′	Hair chaetae finely serrate, in III extremely long; needle chaetae with sharp simple or very finely bifid tip; ventral chaetae of (II) III particularly thick and stout, with upper tooth 2−3 times longer; in the other segments with upper tooth 1.5−2 times longer. L = 3.5−6 mm, n = 13−25 (Fig. 12.4(1−4)) ..... *Pristina* (*P.*) *longiseta* Ehrenberg, 1828 [Cosmopolitan]
3(2)	Dorsal chaetae beginning from II 4
3′	Dorsal chaetae beginning from III or IV, hair chaetae very stout and serrate, by 1−4; needle chaetae by 1−3, simple-pointed; ventral chaetae with longer upper tooth, by 5−10, those in II longer than the rest. L = 3.8−7 mm, n = 10−16. ..... *Pristina* (*P.*) *macrochaeta* Stephenson, 1931 [Near East. Neotropical]
4(3)	Dorsal needle chaeta simple pointed 5
4′	Dorsal needle chaetae bifid 6
5(4)	Hair chaetae very long, serrate with denticle bases are ensheathing the chaeta, 1−4 per bundle; needle chaetae also thin filiform but shorter, by 2−3; ventral chaetae with longer upper tooth, 4−10, in II longer and thinner than remaining; L ≤ 12 mm, n = 15−34 ..... *Pristina* (*P.*) *biserrata* Chen, 1940 [eastern Asia. Neotropics]

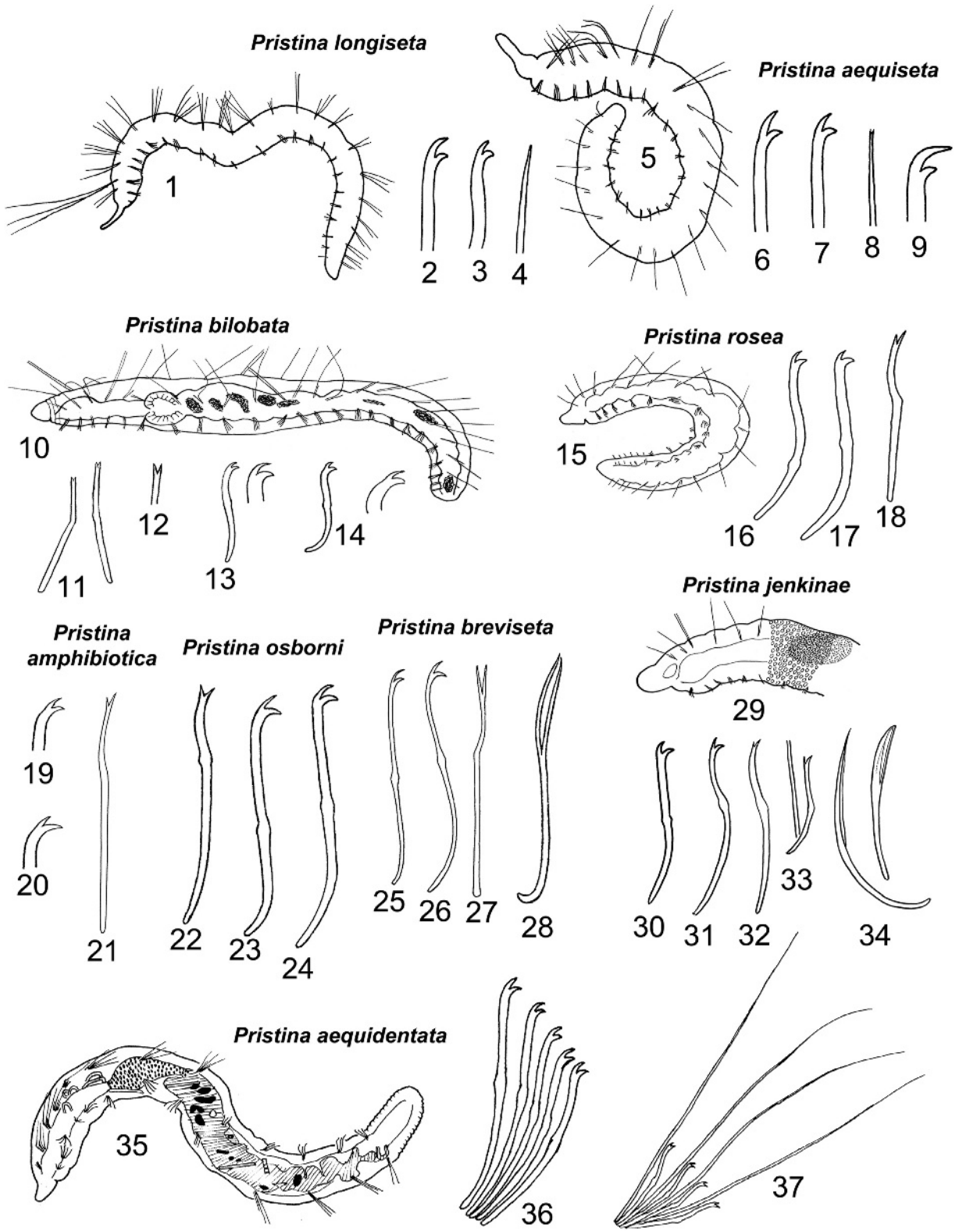


FIGURE 12.4 Pristinidae: (1–4): *Pristina longiseta*: (1) general view, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) needle chaeta; (5—9): *Pristina aequiseta*: (5) general view, (6) anterior ventral chaeta, (7) posterior ventral chaeta, (8) needle chaeta, (9) giant ventral chaeta of IV; (10–14): *Pristina bilobata*: (10) general view, (11, 12) needle chaetae, (13) anterior ventral chaetae, (14) posterior ventral chaetae; (15–18): *Pristina rosea*: (15) general view, (16) anterior ventral chaeta, (17) posterior ventral chaeta, (18) needle chaeta; (19–21): *Pristina amphibiotica*: (19) anterior ventral chaeta, (20) posterior ventral chaeta, (21) needle chaeta; (22—24): *Pristina osborni*, (22) needle chaeta, (23) anterior ventral chaeta, (24) posterior ventral chaeta; (25—28): *Pristina breviseta*, (25) anterior ventral chaeta, (26) posterior ventral chaeta, (27) needle chaeta, (28) genital chaeta; (29—34): *Pristina jenkinae,* (29) general view of anterior end of a sexually mature specimen with clitellum, (30) anterior ventral chaeta, (31) posterior ventral chaeta, (32) needle chaeta, (33) dorsal needle and hair chaetae, (34) genital chaetae; (35–37): *Pristina aequidentata*, (35) general view, (36) ventral bundle, (37) dorsal bundle.

5′ Hair chaetae not very long, 1−4, serrate but not ensheathed by denticles; needle chaetae 1−4, straight; ventral chaetae with longer upper tooth, 2−4 in anterior and up to nine in posterior segments, in II longer and thicker than rest; L = 2−5 mm, n = 16−23 ..... *Pristina* (*P.*) *proboscidea* Beddard, 1896
[nearly cosmopolitan, in warmer countries]

6(4) Needle chaetae with distinct long teeth 7

6′ Needle chaetae with very fine teeth, mostly 1−2; hair chaetae 1−2, finely serrate; ventral chaetae 2−8, with upper tooth length 2× II, but teeth becoming gradually even in posterior segments; in typical form, single giant chaetae (not connected with sexual development), thicker and with particularly long upper tooth, occur instead of ventral bundles in IV−V; giant chaetae are lacking in the *forma foreli*. L = 1.8−8.5 mm, n = 12−26 (Fig. 12.4(5–9)) ..... *Pristina* (*P.*) *aequiseta* Bourne, 1891
[cosmopolitan]

7(6) Hair chaetae smooth 8

7′ Hair chaetae 2−4, serrate; needles 1−3, stout, with equally long parallel teeth; ventral chaetae 4−6, gradually shorter in posterior segments, with slightly longer upper tooth; L = 4−4.5 mm ..... *Pristina* (*P.*) *peruviana* Černosvitov, 1939
[Neotropical. Japan: introduced]

8(7) Hair and needle chaetae one per bundle; needle chaetae teeth equal in anterior segments but upper tooth becomes shorter in posterior ones; ventral chaetae three to five in anterior segments but 1−2, posteriorly; those of II the longest and with longer upper tooth; the latter becomes gradually shorter than the lower one, in posterior segments; tentacle sometimes very short; L = 10−20 mm, n = 18−26 (Fig. 12.4(25–28)) ..... *Pristina* (*P.*) *breviseta* Bourne, 1891
[nearly cosmopolitan]

8′ Hair and needle chaetae 1−2 per bundle; needle chaetae with lower tooth considerably longer than the upper; ventral chaetae teeth equal, four in anterior segments but decreasing in numbers posteriorly; L = 5−7 mm, n = 18−22 ..... *Pristina* (*P.*) *synclites* Stephenson, 1925
[southern hemisphere. The Netherlands: introduced]

9(1) Needle chaetae teeth subequal, or upper tooth slightly longer 10

9′ Needle chaetae upper tooth much shorter or lacking 16

10(9) Needle chaetae bifid, usually without intermediate teeth 11

10′ Needle chaetae usually with 1−2 intermediate denticles, 1−2 per bundle; hair chaetae single, smooth; ventral chaetae 3−6, upper tooth longer than lower in II, and smaller in posterior bundles; L = ∼2 mm, n = 14 ..... *Pristina* (*Pristinella*) *sima* (Marcus, 1944)
[Mediterranean region, Japan. Nearctic, Neotropic]

11(10) Needle chaetae with equal teeth 12

11′ Needle chaetae with longer and thicker upper tooth, 2−5 per bundle; hair chaetae also 2−5, finely serrate; ventral chaetae 4−6, with longer and thinner upper tooth; L = 3−11 mm, n = 12−14 ..... *Pristina* (*Pristinella*) *acuminata* Liang, 1958
[China, Turkey. Nearctic. Neotropical. Oriental]

12(11) Ventral chaetae upper tooth not becoming longer in posterior segments 13

12′ Ventral chaetae 3−4 per bundle, the upper tooth length ≤ lower tooth length in anterior segments but becoming gradually longer backwards; hair chaetae 1−2, pilose; needle chaetae 1−2, with short diverging teeth; L = 1.9 mm ..... *Pristina* (*Pristinella*) *komi* (Popchenko, 1988)
[Russia]

13(12) Needle chaetae teeth more or less diverging 14

13′ Needle chaetae 1−2, with parallel teeth; hair chaetae 1−3, serrate; ventral chaetae 3−8, teeth equal; L = 4−5 mm, n = 18−20 (Fig. 12.4(10–14)) ..... *Pristina* (*Pristinella*) *bilobata* (Bretscher, 1903)
[widespread]

14(13) Needle chaetae with short teeth diverging at an acute angle 15

14′ Needle chaetae with widely diverging teeth, rarely with one to two intermediate denticles; both hair and needle chaetae one per bundle; hair chaetae smooth; ventral chaetae 3−5 anteriorly, 2−3 posteriorly, in II longer and straighter and with longer upper tooth, in the following segments with equally long teeth; L = 1.6−2 mm, n = 12−15 (Fig. 12.4(22–24)) ..... *Pristina* (*Pristinella*) *osborni* (Walton, 1906)
[cosmopolitan]

15(14) Both hair and needle chaetae 4−6 per bundle; hair chaetae smooth; ventral chaetae mostly four (seldom 5−6), with equally long teeth; L = 2−2.9 mm, n = 14−19 (Fig. 12.4(35–37)) ..... *Pristina* (*Pristinella*) *aequidentata* (Liang & Xie, 1997)
[China, Russia]

15′ Both hair and needle chaetae 1−2; hair chaetae serrate; ventral chaetae 4−7 anteriorly, 2−4 posteriorly, upper tooth longer in II−III but becoming gradually equal and shorter posteriorly; L = 1.5−2.5 mm, n = 14(26?) ..... *Pristina* (*Pristinella*) *notopora* Cernosvitov, 1937
[Europe. Afrotropical. Neotropical]

16(9) Needle chaetae upper tooth shorter than lower but always distinct 17

16′ Needle chaetae upper tooth reduced, sometimes even lacking; both hair and needle chaetae 1−2 per bundle; hair chaetae smooth; ventral chaetae 2−5, upper tooth longer in anteriormost segments but becoming gradually equal or shorter posteriorly; L = ~7 mm, n = 20−28 ..... *Pristina* (*Pristinella*) *menoni* (Aiyer, 1930) [widespread]

17(16) Ventral chaetae upper tooth becomes gradually shorter than lower in posterior segments 18

17′ Posterior ventral chaetae teeth equally long 19

18(17) Hair chaetae pilose, anteriorly longer than in posterior segments; both hair and needle chaetae one (seldom two) per bundle; ventral chaetae four (seldom five) in anterior segments, two to three posteriorly; upper tooth slightly longer in anteriormost but shorter in posterior segments; L = 2.5−6 mm ..... *Pristina* (*Pristinella*) *arcaliae* Pop, 1973 [Romania]

18′ Hair chaetae smooth, 1−2 per bundle; needle chaetae also 1−2, the longest and sometimes also thicker than the rest, in IV−V; ventral chaetae 3−6, the upper tooth slightly longer or equal to lower in anteriormost but shorter in posterior segments; L = 3−6 mm, n = 11−12 (Fig. 12.4(19–21)) ..... *Pristina* (*Pristinella*) *amphibiotica* Lastočkin, 1927 [widespread]

19(17) Hair chaetae finely serrate; both the hair and needle chaetae 1−2 per bundle; ventral chaetae 2−5, with longer upper tooth in forebody but with equal teeth posteriorly; L= 4−5.5 mm, n = 16−18 (Fig. 12.4(15–18)] ..... *Pristina* (*Pristinella*) *rosea* (Piguet, 1906) [western Palaearctic. Neotropics]

19′ Hair chaetae smooth; both hair and needle chaetae 1−2 per bundle; ventral chaetae 3−7 in anterior bundles, with upper tooth a bit longer or equal to lower, and 2−3 and with equal teeth posteriorly; L= 2.5−4 mm, n = 11−13 (Fig.12.4(29–34)) ..... *Pristina* (*Pristinella*) *jenkinae* (Stephenson, 1931) [cosmopolitan]

Oligochaeta: Tubificida: Naididae: Genera (excluding Lake Baikal)

A separate key to the Naididae of Lake Baikal is given on p. 387.

1 Dorsal chaetae present at least in some posterior segments; ventral chaetae present also in III−V; prostomium well developed 2

1′ Dorsal chaetae entirely lacking (but can be sometimes rudimentary in one species); first five segments fused, bearing a single pair of ventral bundles (II), the next bundles appearing only in VI; prostomium more or less reduced in most species, mouth terminal, pharynx cylindrical and thick-walled, followed by a spacious stomach; mature male pores and penial chaetae in VI ..... ***Chaetogaster*** **[p. 375]**

2(1) No hair chaetae 3

2′ Hair chaetae present in dorsal bundles 7

3(2) Dorsal bundles beginning further posteriorly of III 4

3′ Dorsal bundles beginning from III. All chaetae similar, bifid, fine, with equal teeth; segment III prolonged; stomach in V−VI; eyes absent; mature male pores in VI; no penial chaetae; does not swim ..... ***Amphichaeta*** **[p. 376]**

4(3) Dorsal bundles beginning from VI (seldom farther backwards). In mature individuals male pores and (sometimes) penial chaetae in VI. Eyes present or lacking 5

4′ Dorsal bundles beginning from V. In mature individuals male pores (with or without penial chaetae) in V. No eyes ..... ***Paranais*** **[p. 376]**

5(4) Uniform bifid or pectinate chaetae in dorsal and ventral bundles 6

5′ Single thick, baciliform chaetae with rounded or obtusely bifid tip, in dorsal bundles beginning usually from VI (but sometimes lacking in many segments). Ventral bifids with about equal teeth. Dark transverse stripes can occur on anterior segments. Eyes present. L = 6−36 mm, n = 23−51 (Fig. 12.6(3−5)) ..... *Ophidonais serpentina* (Müller, 1774) [Holarctic. Neotropics]

6(5) In mature individuals one to four saber-shaped spermathecal chaetae with simple sharp tip in the ventral bundles of V, sometimes accompanied by 1−2 ordinary bifids. No penial chaetae. Both dorsal and ventral chaetae with 1−5 fine intermediate denticles; the main teeth of equal length or the upper tooth slightly longer. Ventral chaetae in II 3−5 per bundle, in subsequent segments by 3−8. Dorsal chaetae 1−6 per bundle. No eyes. L = 3−6.5 mm ..... *Piguetiella denticulata* Liang & Xie, 1997 [eastern Asia]

6′ No spermathecal chaetae but penial chaetae present in mature individuals. Eyes present ..... ***Uncinais*** **[p. 378]**

7(2) No dorsal digitiform gills on forebody 8

7′ Dorsal chaetal bundles from VI onwards, mostly included into long digitiform gills, consisting of 1−5 very long hair chaetae and 1−2 simple-pointed or finely bifid needle chaetae. Ventral chaetae 3−5 per bundle, bifid with teeth of equal length. In mature individuals simple-pointed penial chaetae, 2−3 per bundle, in VI. Forebody transversely striped with brown pigment. No eyes. L = 5−50 mm, n = 29−70 (Fig. 12.6(6−9)) ..... *Branchiodrilus hortensis* (Stephenson, 1910) [Afrotropical, Oriental, Oceania. Introduced: Europe]

8(7) Posterior end with branchial disk surrounding anus and bearing digitiform or foliform gills (the latter are usually contracted and shapeless in irritated or killed worms); gills sometimes reduced. Dorsal bundles consisting of 1−2 smooth hair chaetae and 1−2 bifid needles, pectinate or palmate chaetae. No modified genital chaetae. No eyes. Constructing portable or attached tubes from secretion and attached particles; able to swim 9

8′ Posterior end with small, sometimes slightly dorsal anus, without any gills. Dorsal chaetae can be of different shape. Genital chaetae and eyes can be present or absent 10

9(8) Branchial disk bearing, besides contractile gills, one pair of noncontractile palps well visible even in preserved worms. Hair chaetae smooth ..... ***Aulophorus*** **[p. 378]**

9′ No palps on branchial disk; only short foliate or digitiform, contractile gills, sometimes reduced. Hair chaetae smooth or, in some species, plumose ..... ***Dero*** **[p. 379]**

10(8) Prostomium with proboscis (tentacle). Dorsal bundles beginning from VI, needle chaetae simple pointed, sharp 11

10′ Prostomium simple, without proboscis. Eyes present or absent 13

11(10) Hair and needle chaetae numerous and thin. Proboscis attached to the obtuse prostomium short and thin 12

11′ Hair chaetae 1−3 per bundle, thick and stiff. Ventral bifids with two seemingly broken portions in their proximal half, with upper tooth much longer and distally curved. Proboscis very long. Eyes present. Swims well ..... ***Stylaria*** **[p. 381]**

12(11) Hair chaetae of VI−VIII extremely long. Ventral chaetae lacking in IV and V. Eyes present. Swims but also constructing tubes attached to water plants. L = 2−7.5 mm, n = 14−21 (Fig. 12.7(6−9)) ..... *Ripistes parasita* (Schmidt, 1847) [Holarctic]

12′ No extremely long chaetae in VI−VIII. Full set of chaetae in II−V. Ventral chaetae present in all segments. Eyes present or absent. Does not swim. L = 8−10 mm, n = = ∼32 (Fig. 12.7(10−12)) ..... *Arcteonais lomondi* (Martin, 1907) [Holarctic]

13(10) Body armored with foreign matter particles adhering to cutaneous glands 14

13′ Body surface smooth 15

14(13) Dorsal hair and needle chaetae beginning from VI, both by 1−2. Hair chaetae of VI considerably longer than those of the subsequent segments. Tip of needle chaetae forming a small knob. Ventral chaetae by 2−5, with slightly longer and thinner upper tooth. Eyes present. L = 2−20 mm, n = 19−29 (Fig. 12.7(13−15)) ..... *Slavina appendiculata* (Udekem, 1855) [cosmopolitan]

14′ Dorsal bundles beginning from II, consisting of 3−4 hair and 3−4 straight, simple-pointed needle chaetae in anterior segments, these numbers decreasing to 1−2 posteriorly. Ventral chaetae anteriorly up to four, posteriorly only by one, with longer upper tooth, the difference in teeth length increasing backwards. No eyes. L = 2−6 mm, n = 12−20 (Fig. 12.7(16−18)) ..... *Stephensoniana trivandrana* (Aiyer, 1926) [Israel. Eastern Palaearctic.Circumtropical. Nearctic]

15(13) Dorsal bundles beginning in anterior segments (II−VI, seldom VII−XII) 16

15′ Dorsal bundles beginning from XVIII−XX, in each bundle one short hair chaeta and one bifid crotchet similar to the ventral ones, with 1.5 times longer upper tooth. Ventral chaetae by 2−4, teeth longer in the anterior half of body but becoming gradually shorter posteriorly. No eyes. L = 5−20 mm, n = 31−36 (Fig. 12.8(14−17)) ..... *Haemonais waldvogeli* Bretscher, 1900 [cosmopolitan]

16(15) Dorsal bundles beginning from VI (seldom V or VII); eyes present or absent 17

16′ Dorsal bundles beginning from III or II. No eyes. Paratomy not observed ..... ***Bratislavia*** **[p. 381]**

17(16) Full set of ventral chaetae in II−V. Hair chaetae mostly smooth (seldom finely serrate or pilose) 18

17′ Ventral chaetae absent in V, or also in IV, leaving a false impression that the dorsal chaetae begin from V or IV (in fact, they begin from VI). Hair chaetae thick, serrate with two rows of rough denticles on their convex side; needle chaetae much thinner and simple-pointed. In mature individuals single-pointed penial chaetae by one per bundle. Eyes present ..... ***Vejdovskyella*** (in part) **[p. 381]**

18(17) No enlarged ventral chaetae (besides modified genital chaetae) 19

18′ Ventral chaetae in VI (or also in some next segments) thick and curved, with upper tooth split into 2−3 denticles. ..... ***Vejdovskyella*** (in part) **[p. 381]**

19(18) Chaetal pattern different than below. Hair chaetae smooth; ventral bundles present in all segments. Prostomium usually not very short, often conical, sometimes bearing eyes 20

19′ Dorsal bundles in VI consisting of thick, mucronate hair chaetae and thin simple-pointed needle chaetae, both 1−2 per bundle. Ventral chaetae 3−4 per bundle in II−V, 2−3 per bundle in following segments, all of similar shape, with teeth of equal thickness but upper tooth 2−2.5 times longer than lower. ..... ***Vejdovskyella*** (in part) **[p. 381]**

20(19) Dorsal shorter (needle) chaetae sigmoid and bifid like the ventral crotchets 21

20′ Dorsal needle chaetae much different from the ventral crotchets, usually thinner and straighter, either simple pointed or with fine teeth 24

21(20) Dorsal sigmoid crotchets finer and straighter than the ventral ones. No eyes 22

21′ Dorsal and ventral bifid crotchets of similar shape and size. Eyes present 23

22(21) Dorsal sigmoid crotchets with short equal teeth, by 2−6 per bundle together with 2−6 hair chaetae. Ventral chaetae by 5−10, with slightly longer upper tooth, similar in the anterior and posterior body region. In mature individuals single-pointed, hooked penial chaetae by 1−3. No eyes. L = 3−10 mm. n = 11−27 (Fig. 12.8(10−13)) ..... *Specaria josinae* (Vejdovský, 1884) [Holarctic]

22′ Dorsal sigmoid chaetae with one curved hair chaeta (shorter than body diameter) and one sigmoid crotchet, with considerably longer upper tooth. Ventral chaetae in II−V by three, in midbody by four to five, in hindbody by 2−3 per bundle, all with much longer upper tooth; in II−VI longer and with long parallel teeth, beginning from VII shorter, more curved, and teeth diverging on acute angle. No penial chaetae in mature individuals. L = 2.5−3 mm. Thermal waters?..... "*Nais*" *bihorensis* Pop, 1971 species incertae sedis [Romania]

23(21) Dorsal bundles beginning always from VI, with none to three very fine and short hair chaetae and 2−6 crotchets, the latter with the upper tooth slightly longer. Ventral chaetae uniform, slightly longer, by 3−9. No penial chaetae but mucronate spermathecal chaetae in V of mature individuals, simple-pointed or with reduced lower tooth, by 1−2. L = 3−7 mm, n = 17−24 (Fig. 12.8(1−5)) ..... *Piguetiella blanci* (Piguet, 1906) [western Palaearctic. Nearctic: introduced(?)]

23′ Dorsal bundles beginning from VI or VII−XII, consisting of one bifid chaeta with longer and straighter upper tooth, and of a slightly longer and thinner, bent hair chaeta. Ventral bundles in II by 3−5, with upper tooth considerably longer; in III−IV by two, and in the following segments by 1−4. Those of II−V slightly thinner than the rest, and with upper tooth considerably longer; further backward the teeth are of equal length. Mature individuals not known. L = 3−7 mm, n = 18−28(50?) (Fig. 12.8(6−9))..... "*Piguetiella*" *amurensis* Sokolskaja, 1958, species incertae sedis [eastern Palaearctic]

24(20) Vegetative reproduction by architomy (fragmentation, without budding zones). Ventral chaetae of II−V only slightly different from those of following segments. No eyes ..... ***Allonais*** **[p. 383]**

24′ Vegetative reproduction by paratomy (with forming budding zones before splitting). Ventral chaetae of II−V mostly longer, thinner and straighter than those of following segments. .....Eyes usually present ***Nais*** **[p. 383]**

Oligochaeta: Tubificida: Naididae: *Chaetogaster*: Species (excluding Lake Baikal)

1 Comparatively big worms: chaetae of II usually more than 125 μm long; all chaetae bifid, with slightly longer upper tooth; prostomium absent, often a notch in its place 2

1′ Smaller worms: chaetae of II never longer than 125 μm 3

2(1) Large worm: chaetae of II 200−350 μm long, 2−20 per bundle anteriorly; L = 2.5−25 mm, n = 9−12 (Fig. 12.5(1−4)) ..... *Chaetogaster diaphanus* (Gruithuisen, 1828) [cosmopolitan]

2′ Worm of medium size: chaetae of II 108−165 μm long, 4−13 per bundle; stomach surrounded by about 20 separate transverse blood vessels. L = 2.5−7 mm, n = 8−9 ..... *Chaetogaster cristallinus* Vejdovský, 1884 [nearly cosmopolitan]

3(1) At least some chaetae simple-pointed, or with much shorter lower tooth 4

3′ All chaetae distinctly bifid 6

4(3) Only simple-pointed chaetae in II but combined with bifid ones in other segments 5

4′ All chaetae simple-pointed or with a very thin lower tooth adherent to the upper one. In II, 9−10 chaetae per bundle, from VI on, 5−8 much thinner chaetae. L = ∼0.7 mm (Fig. 12.5(10, 11))..... *Chaetogaster setosus* Svetlov, 1925 [western Palaearctic. Nearctic]

5(4) In II 6−7 uniformly sigmoid, simple pointed, chaetae per bundle; from VI on, 4−6 (seldom up to 10) chaetae, most of them simple-pointed but 1−2 with distinct lower tooth. L = 0.8−1.1 mm, n = 9−11 ..... *Chaetogaster diversisetosus* Šporka, 1983 [Europe: Danube River]

5′ In II 5−6 simple pointed, sigmoid chaetae per bundle, combined with one shorter, thicker and straighter chaeta; from VI on, four chaetae per bundle, with rudimentary lower tooth; L = 0.5−0.8 mm .....*Chaetogaster intermedius* Akinschina, 1984 [Russia: Lake Baikal and Angara River]

6(3) Chaetae upper tooth slightly longer or equal to lower one; if slightly shorter, then not erect 7

6′ Chaetae with shorter, erect upper tooth; II with 1−2 chaetae per bundle, from VI on, 4−6; L = 1.2−1.4 mm, n = 8; rivers ..... *Chaetogaster krasnopolskiae* Lastočkin, 1937 [eastern Europe]

7(6) Chaetae upper tooth slightly longer, or equal to lower one, not hooked 8

7′ Chaetae upper tooth equal to, or slightly shorter than lower one; both teeth long and hooked; in II, 8−20 chaetae per bundle, in posterior segments their number can decrease; commensal or (as subspecies *vaghini* Gruffydd, 1965) kidney parasite of freshwater snails; L = 0.7−5 mm, n = 8−9 (Fig. 12.5(8, 9)) ..... *Chaetogaster limnaei* Baer, 1827 [cosmopolitan]

8(7) Prostomium vestigial; in II, 3−9 chaetae per bundle, from VI on, 3−6; L = 0.8−2 mm, n = 8−9 ..... *Chaetogaster langi* Bretscher, 1896
[nearly cosmopolitan]

8′ Prostomium developed, conical. In II, 4−8 chaetae per bundle, from VI on, 3−7; some specimens (described from France as *Pseudochaetogaster longemeri* Lafont, 1981), vestigial dorsal chaetae, two per bundle, have been found from VI on. L = 1−5 mm, n = 8 (Fig. 12.5(5−7)) ..... *Chaetogaster diastrophus* (Gruithuisen, 1828)
[cosmopolitan]

Oligochaeta: Tubificida: Naididae: *Amphichaeta*: Species (excluding Lake Baikal)

1 No proboscis 2

1′ Prostomium extended to a short proboscis; dorsal chaetae in III and ventral chaetae in II−III three per bundle; in all bundles of IV−V chaetae by two, posteriorly again by three; all chaetae with thinner and shorter upper tooth; L = 0.8−1.2 mm ..... *Amphichaeta rostrifera* Akinschina, 1984
[Russia]

2(1) Usually more than three chaetae in the ventral bundles of II 3

2′ Ventral chaetae in all segments usually by three per bundle, the dorsal chaetae in III by four, beginning from IV by 2−3; both branches of the ventral vessel making a loop in prostomium; L = 2.5−3 mm, n = 8−10, mostly eight ..... *Amphichaeta asiatica* Liang, 1958
[China]

3(2) Chaetal teeth equally long 4

3′ At least in the most anterior bundles chaetae with shorter upper teeth 5

4(3) Dorsal chaetae of III five per bundle, of IV and V two per bundle, and beginning from VI 1−4 per bundle. Ventral bundles of II and III with four chaetae, of IV and V with two chaetae, and in the rear segments with 1−4 chaetae. L ≤ 4 mm, n = 9−11 (Fig. 12.5(12, 13)) ..... *Amphichaeta leydigi* Tauber, 1879
[Palaearctic. Nearctic. Neotropics]

4′ Dorsal chaetae of III and ventral chaetae of II usually four per bundle, the rest of chaetae usually by three; L = >1.5 mm; n = 9; brackish water ..... *Amphichaeta sannio* Kallstenius, 1892
[western Palaearctic]

5(4) Dorsal chaetae of III less than seven per bundle; distal portion of chaetae not widened; chaetal teeth becoming equally long, or the upper tooth slightly longer in posterior segments; pharynx walls thick 6

5′ All chaetae long and sigmoid, with slightly shorter upper tooth; ventral chaetae of II−III 3−4 per bundle, dorsal chaetae of III by seven; chaetae of II−III widened in their distal portion; in IV−V chaetae by two, in the following segments by 3−4; mouth segment (I) rudimentary; pharynx with thin wall and wide lumen ..... *Amphichaeta nikae* Semernoy, 2004
[Russia]

6(5) Ventral chaetae of II by 4−7 per bundle, with upper tooth up to 1.5−2 times shorter than the lower; in III chaetae by 4−6, in the following segments by 3−4. Pharyngeal musculature very thick, fused with the body wall. Prostomium either oval or prolonged. L = 2.3−5 mm ..... *Amphichaeta magna* Sokolskaja, 1962
[Russia]

6′ Ventral chaetae of II by 3−5 per bundle, with shorter upper tooth; chaetae of III by 3−5, those of the IV−V by two, and of the following segments by three. Anterior chaetae relatively straight, and thick, the posterior ones sigmoid. L = 0.9−1.1 mm ..... *Amphichaeta annae* Semernoy, 2004
[Russia]

Oligochaeta: Tubificida: Naididae: *Paranais*: Species

1 Body surface usually dark or striped due to detritus adhering between the transverse epidermal ridges 2

1′ Body surface smooth 3

2(1) All chaetae with upper tooth at least twice as long as lower one; their number in ventral bundles of II two to four, in dorsal bundles of V 1−3, further posteriorly only 1−2; in mature individuals penial chaetae of almost similar shape; L = 2.7−6 mm, n = 9−13 (Fig. 12.5(14, 15)); fresh and brackish water ..... *Paranais frici* Hrabe, 1941
[cosmopolitan]

2′ Ventral chaetae of II 5−7 per bundle, with upper tooth twice longer than lower. Dorsal chaetae in V by 4−6. In posterior segments the segment number decreases to 3−4, and the difference in length of teeth diminishes. No modified penial chaetae but 2−3 ordinary bifid crotchets at male pores in V. L = 3.5−5 mm; brackish water ..... *Paranais birsteini* Sokolskaja, 1971
[northern Pacific Rim. North Africa]

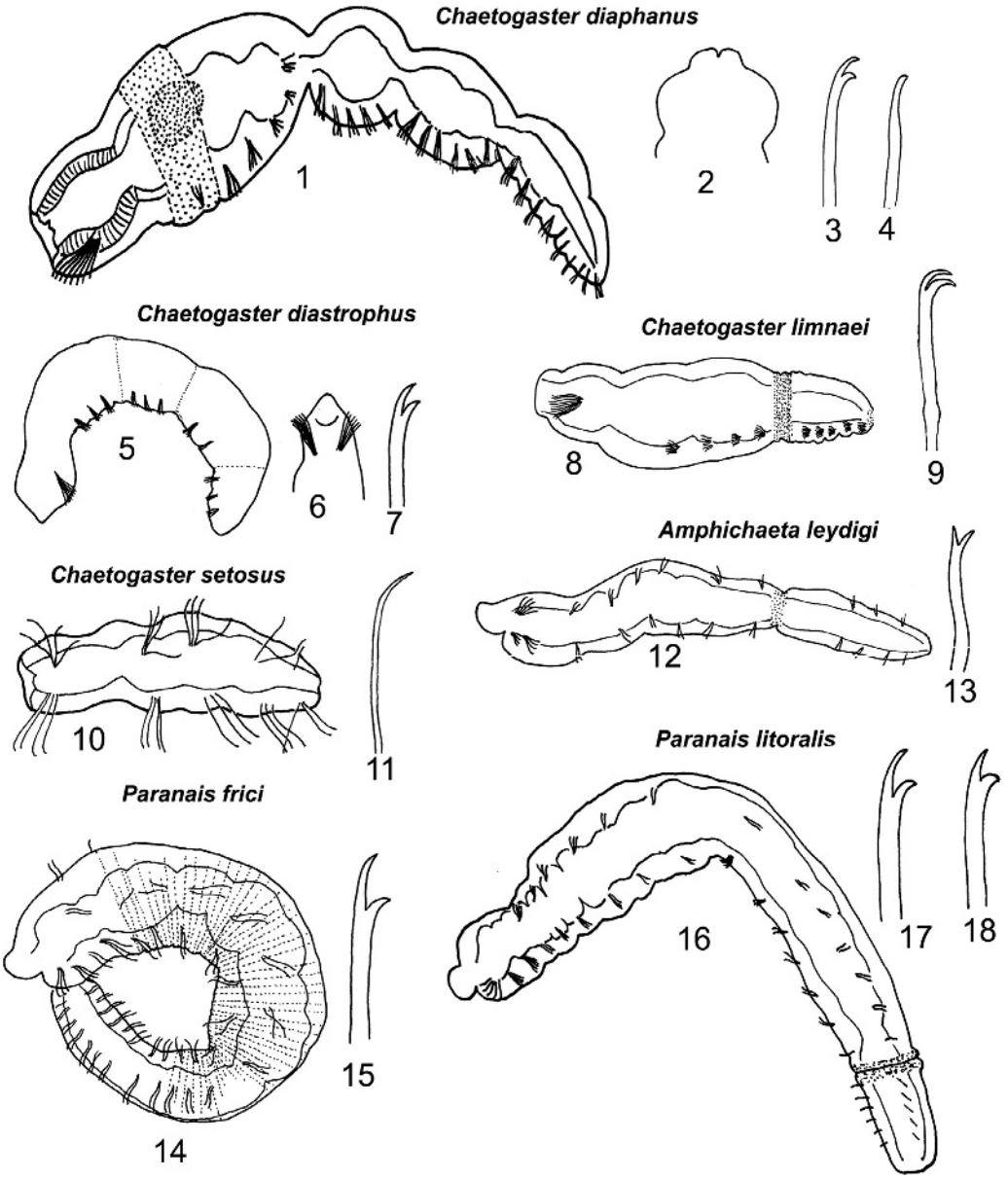


FIGURE 12.5 Naididae I: (1–4): *Chaetogaster diaphanus:* (1) general view of a chain of four zooids with clitellum and an egg, (2) dorsal view of anterior end, (3) ordinary chaeta, (4) penial chaeta; (5–7): *Chaetogaster diastrophus*: (5) general view of a chain of four zooids, (6) ventral view of anterior end, (7) chaeta; (8, 9): *Chaetogaster limnaei:* (8) general view of a chain of two zooids, (9) chaeta; (10, 11): *Chaetogaster setosus*: (10) general view of a single zooid, (11) chaeta; (12, 13): *Amphichaeta leydigi*: (12) general view of a chain of two zooids, (13) chaeta; (14, 15): *Paranais frici*: (14) general view of a single individual, (15) chaeta; (16–18): *Paranais litoralis*: (16) general view of a chain of two zooids, (17) chaeta of II, (18) posterior chaeta.

3(1) Ventral chaetae of II with upper tooth about twice as long as the lower. In mature individuals penial chaetae by two per bundle, always bifid 4

3′ Ventral chaetae of II with upper tooth considerably less than twice as long as the lower. In mature individuals penial chaetae usually more than two per bundle, simple-pointed, bifid, or lacking 5

4(3) Ventral chaetae of II 5–6 per bundle, longer than the rest; posterior 2–4 chaetae per bundle, tooth length becoming gradually equal in posterior segments. Dorsal chaetae by 2–4, slightly thinner than ventral, with teeth equally long. In mature individuals penial chaetae by two, bifid, straighter than the rest and with strongly distal nodulus. L = 6–10 mm, n = 14; slightly brackish water lagoons ....*Paranais botniensis* Sperber, 1948 [Baltic Sea]

4′ Ventral chaetae of II 5−7 per bundle, with longer (less than twice as long) upper tooth. Ventral chaetae in III−IV by 2−4, posterior by 1−3; dorsal chaetae in V by 2−4, posterior by 1−3; in all of them teeth of equal length or the upper tooth slightly longer. In mature individuals penial chaetae two (seldom three) per bundle, similar to the chaetae of II but longer. L = 5−6 mm; slightly brackish water ..... *Paranais tjupensis* Finogenova, 1977 [Kyrgyzstan]

5(3) Ventral chaetae of II with upper tooth 1.5 times longer than lower, further posterior teeth becoming gradually subequal; penial chaetae present in mature individuals 6

5′ Ventral chaetae of II with equally long chaetae, posteriorly upper tooth shorter; no modified penial chaetae in mature individuals 7

6(5) Ventral chaetae of II 5−7 per bundle; more posterior 2−4 chaetae both in ventral and dorsal bundles, teeth becoming gradually equal; mature penial chaetae in V, with 2−4 per bundle, with a simple bent end; L = 2−14 mm, n = 14−17; marine littoral, brackish water, and fresh water receiving saline pollution (Fig. 12.5(16−18)) ..... *Paranais litoralis* (Müller, 1784) [cosmopolitan]

6′ Ventral chaetae of II 4−7 per bundle; more posterior 2−4 chaetae both in ventral and dorsal bundles, teeth becoming gradually equal or slightly shorter; mature penial chaetae in V, 4−5 per bundle, with a strongly bent bifid end; L = 2.8−5 mm, n = 17−22; brackish lakes ..... *Paranais orientalis* Sokolskaja, 1964 [Russia]

7(5) Ventral chaetae of II 5−6 per bundle, further posterior 3−4 chaetae both in ventral and dorsal bundles; L = 4−4.5 mm, n = 17−24; fresh and brackish water ..... *Paranais simplex* Hrabě, 1936 [western Palaearctic, Ponto-Caspian Basin]

7′ Ventral chaetae of II 8−10 per bundle, posteriors gradually decreasing from 5−6 to three; in dorsal bundles the number of chaetae decreasing from 4−3, respectively; L = 2−3 mm, n = 20−25; slightly brackish water ..... *Paranais multisetosa* Finogenova, 1972 [Ukraine]

Oligochaeta: Tubificida: Naididae: *Uncinais*: Species (excluding Lake Baikal)

1 No intermediate denticles in chaetae; eyes present 2

1′ Both dorsal and ventral chaetae with 2−4 fine intermediate denticles; main teeth length equal; ventral chaetae 4−6, dorsal chaetae 3−5 per bundle; no eyes; adults not known; L ≥ 4 mm ..... *Uncinais golyschkinae* Akinschina, 1984 [Russia]

2(1) All chaetae with upper tooth slightly longer (the difference decreasing posteriorly); II with ventral bundles with 2−7 chaetae; 2−4 chaetae in bundles of following segments; mature individuals 2−3 blunt-tipped penial chaetae at male pores in VI; forebody dorsally sometimes with pigment spots; L = 5−18 mm, n = 19−27; freshwater (Fig. 12.6(1, 2)) ..... *Uncinais uncinata* (Ørsted, 1842) [Palaearctic. Nearctic. Neotropics]

2′ Chaetae with teeth equal or, in posterior segments, with slightly shorter upper tooth; mature individuals 3−4 blunt-tipped penial chaetae at male pores in VI; L = 2.8−5 mm ..... *Uncinais minor* Sokolskaja, 1962 [Russia]

Oligochaeta: Tubificida: Naididae: *Aulophorus*: Species

1 Dorsal bundles beginning from V 2

1′ Dorsal bundles beginning from VI; gills long, digitiform 3

2(1) Dorsal bundles consisting of 1−2 hair chaetae and 1−2 bifid needle chaetae without intermediate denticles, the teeth being of equal length or upper tooth slightly shorter; ventral chaetae of II−IV 2−5 per bundle, longer than rest, with longer upper tooth; beginning from V, 2−3 and with equal teeth or upper shorter; branchial disk with 3−4 pairs of foliate gills; palps slightly diverging; L = 6−20 mm, n = 15−22 (Fig. 12.6(15−19)) ..... *Aulophorus furcatus* (Müller, 1774) [cosmopolitan]

2′ Dorsal bundles consisting of 1−2 hair chaetae and 1−2 bifid needle chaetae with 2−4 intermediate denticles; II−IV ventral chaetae 3−4 per bundle, in following segments 2−5, with equally long teeth; branchial disk with four pairs of gills; palps diverging; L = 12−16 mm ..... *Aulophorus pectinatus* Stephenson, 1931 [China. Nearctic. Neotropics. Afrotropical. Oriental]

3(1) Dorsal bundles of 1−2 modified palmate or spatulate chaetae from at least IX onwards, besides one hair chaeta 4

3′ Dorsal bundles of one hair chaeta and one bifid needle chaeta with distal tooth slightly longer and thicker; ventral chaetae of II−V 4−6 per bundle, longer and straighter than the rest, with upper tooth length two times and slightly thinner than lower; following segments with ventral chaetae 3−5, upper tooth thinner and slightly shorter; five pairs of long, digitiform gills; palps strongly diverging; L = 2−7 mm, n = 17−19 ..... *Aulophorus varians* Liang, 1958 [China]

4(3) Branchial disk with at least two pairs of gills in addition to palps; dorsal chaetae with needles broadly palmate 5

4′ Branchial disk with one median gill flanked by two lateral longer palps; dorsal bundles consisting of one hair chaeta and one needle, simple pointed in VI–VIII, with spatulate distal end from IX onwards; ventral chaetae of II–V 6–9 per bundle, longer than rest, with upper tooth 2.5 times longer than lower; those of following segments four to six, with lower tooth thicker and longer than upper; L = 3 mm, n = 28 ..... *Aulophorus opistocystoides* Nesemann, Shah & Tachamo, 2007 [Nepal]

5(4) Dorsal bundles consisting of one hair chaeta and one palmate chaeta with strongly diverging teeth and broad, obliquely cut thin web 6

5′ Dorsal bundles consisting of one hair chaeta and 1–2 narrowly palmate chaetae with long teeth and connecting them web which may be ribbed; ventral chaetae of II–V 3–9 per bundle, longer than the rest, with longer upper tooth; those of following segments by 3–7, with upper tooth shorter; gills cylindrical, in three pairs; L = 2–5 mm, n = 13–18 .... *Aulophorus tonkinensis* (Vejdovský, 1894) [China. Japan. Circumtropical]

6(5) Gills long, cylindrical, 2–3 pairs; palps long and parallel; ventral chaetae of II–V 4–7 per bundle, more than double the length of rest and less curved, with upper tooth 1.5–2 times longer and three times thinner; remaining ventral chaetae 2–4, with upper tooth thinner and half as long as the lower; L = 2.75 mm, n = 16–18 ..... *Aulophorus flabelliger* Stephenson, 1931 [Japan. Nearctic. Palaeotropical]

6′ Branchial disk with seven gills, the unpaired gill middorsal; ventral chaetae of II–V 3–5 per bundle, about twice as long as the rest, with longer distal tooth; remaining ventral chaetae 3–4, with very short and thin upper tooth; L = 5–8 mm, n = 16–17 .... *Aulophorus heptabrachionus* Liang, 1958 [China]

Oligochaeta: Tubificida: Naididae: *Dero*: Species

1 Dorsal bundles beginning from VI; ventral chaetae of II–V longer and straighter than the rest 2

1′ Dorsal bundles beginning from IV, consisting of 1–2 hair chaetae and 1–2 needle chaetae with slightly longer upper tooth; ventral chaetae in foremost segments 3–7 per bundle, with teeth of equal thickness but the upper tooth 1.5–2 times longer; posterior chaetae becoming gradually shorter, length of teeth equal but lower tooth growing thicker; five pairs of gills, of different shape; L = 10–32 mm, n = 18–53 (Fig. 12.6(25–30)) ..... *Dero dorsalis* Ferronière, 1899 [Palaearctic. Oriental]

2(1) Gill pairs <3 (two small nodiform gills or gills reduced) in branchial disk; needles trifid or bifid with numerous intermediate minute teeth 3

2′ Gill pairs three or four, well developed; dorsal bundles consisting usually of one hair and one needle chaeta; needles bifid or simple pointed 4

3(2) Dorsal bundles consist of one unilaterally plumose hair chaeta with long barbs, and one trifid needle chaeta; ventral chaetae of II–V four per bundle, with longer and thinner upper tooth; those of following segments by 2–4, with shorter upper tooth; two pairs of small nodiform gills not projecting beyond margin of the branchial disk; L = ~2 mm, n = 14–18 ..... *Dero pectinata* Aiyer, 1930 [Azores. Circumtropical]

3′ Gills reduced, numerous low swellings on the edge of small branchial disk; dorsal bundles consisting of one hair and 1–2 needle chaetae, the latter with short, stout and diverging teeth, and numerous, minute, intermediate teeth; ventral chaetae in II–V, 3–4 per bundle, teeth equally thick but the upper one much longer; following segments ventral chaetae with much thinner and slightly shorter upper tooth; L = ~3 mm, n = 12–16 ..... *Dero raviensis* (Stephenson, 1914) [Mauritania. Circumtropical]

4(2) Mostly four pairs of foliate gills; needles simple pointed or bifid with distinctly longer and straighter upper tooth 5

4′ Mostly three pairs of short gills, those of the first (dorsal) pair foliate or reduced, the subsequent ones digitiform; needles with equally short teeth 6

5(4) Needles simple pointed, bayonet-shaped, ventral chaetae of II–V, 2–4 per bundle, with upper tooth twice as long as lower one. In the following segments ventral chaetae by four, with teeth of same length and lower tooth thicker than upper one; L = 10(14) mm, n = 53 ..... *Dero phewatalensis* Nesemann & Sharma, 2007 [Nepal]

5′ Needle chaetae bifid with distinctly longer and straighter upper tooth; ventral chaetae in II–V, 3–6 per bundle, teeth equally thick but the upper one 1.5–2 times longer; following segments ventral chaetae by 2–5, with upper tooth only slightly longer than lower; L = 5–36 mm, n = 12–34 (Fig. 12.6(10–14)) ..... *Dero digitata* (Müller, 1774) [cosmopolitan]

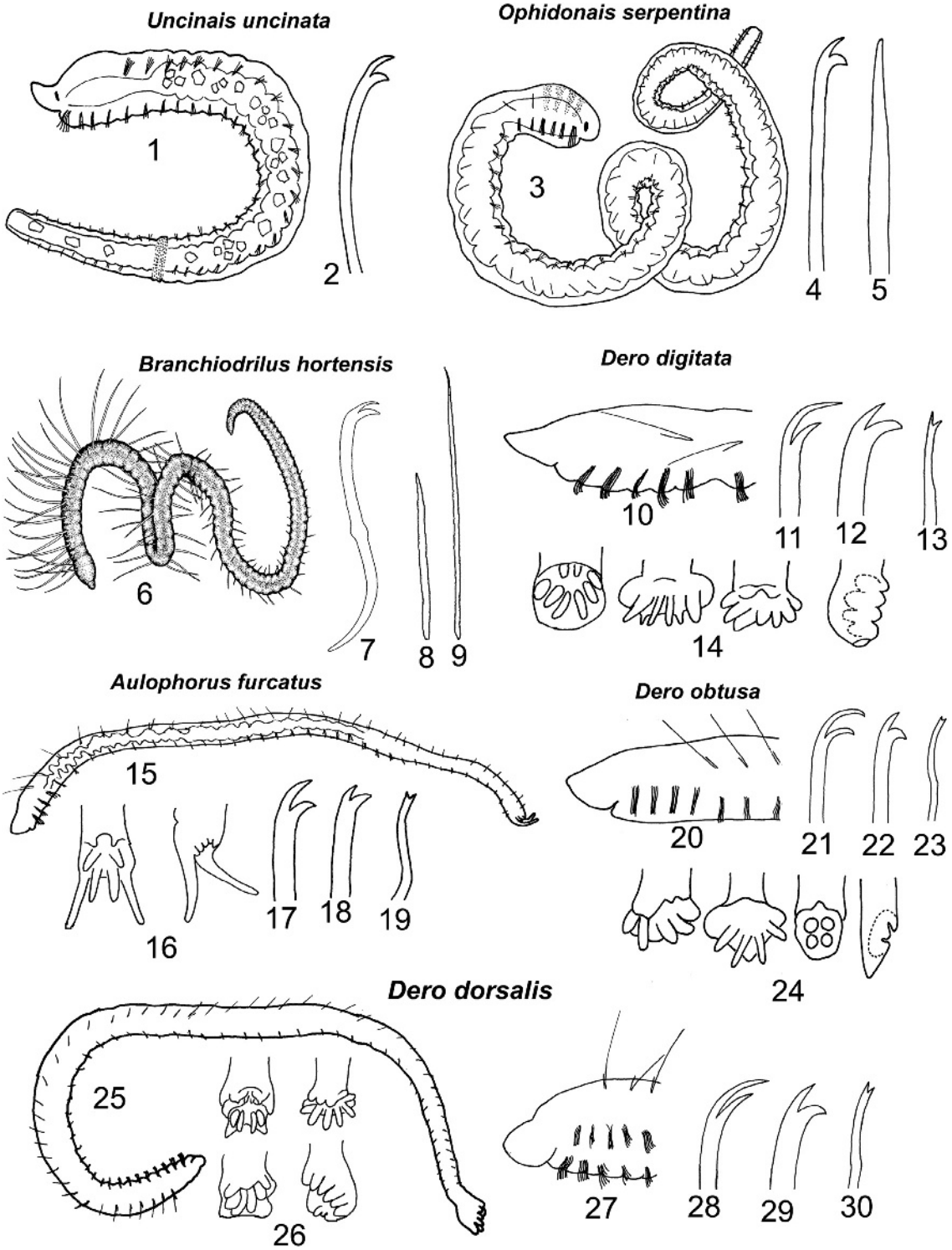


FIGURE 12.6 Naididae II: (1, 2): *Uncinais uncinata*: (1) general view of a chain of two zooids, (2) chaeta; (3–5): *Ophidonais serpentina:* (3) general view, (4) ventral chaeta, (5) dorsal chaeta; (6–9): *Branchiodrilus hortensis*: (6) general view, (7) ventral chaeta, (8) needle chaeta, (9) hair chaeta; (10–14): *Dero digitata:* (10) anterior end, (11) anterior ventral chaeta, (12) posterior ventral chaeta, (13) needle chaeta, (14) different aspects of branchial disk; (15–19): *Aulophorus furcatus*: (15) general view, (16) different aspects of branchial disk, (17) anterior ventral chaeta, (18) posterior ventral chaeta, (19) needle chaeta; (20–24): *Dero obtusa*: (20) anterior end, (21) anterior ventral chaeta, (22) posterior ventral chaeta, (23) needle chaeta, (24) different aspects of branchial disk; (25–30): *Dero dorsalis:* (25) general view, (26) different aspects of branchial disk, (27) anterior end, (28) anterior ventral chaeta, (29) posterior ventral chaeta, (30) needle chaeta.

6(4) Branchial disk short, posterior gills reaching its end; L = 5−19 mm, n = 18−29 (Fig. 12.6(20−24)) ..... *Dero obtusa* Udekem, 1855 [nearly cosmopolitan]

6′ Branchial disk much longer than the short gills, leaving its posterior half free; L = 2.5−10 mm, n = 14 ..... *Dero nivea* Aiyer, 1929 [cosmopolitan]

Oligochaeta: Tubificida: Naididae: *Stylaria*: Species

1 Prostomium with short protruding lobe on either side of proboscis; L = 5.5−18 mm, n = 15−35 (Fig. 12.7(1−4)) ..... *Stylaria lacustris* (Linnaeus, 1767) [Holarctic. Neotropical. Afrotropical]

1′ Prostomium gradually transiting into proboscis, without lateral appendages; L ≤ 15 mm, n = 15−34 (Fig. 12.7(5)) ..... *Stylaria fossularis* Leidy, 1852 [eastern Palaearctic. Nearctic. Afrotropical. Australia]

Oligochaeta: Tubificida: Naididae: *Bratislavia*: Species

1 Dorsal bundles beginning always from III, needle chaetae bifid 2

1′ Dorsal bundles beginning either from II or III, with one very fine smooth hair chaeta and one stout simple-pointed sigmoid needle chaeta with distinct nodulus; hair chaetae occasionally absent in anteriormost segments; ventral chaetae 3−4 per bundle, with distal tooth twice longer in anterior segments but with subequal teeth posteriorly; L = 4−9 mm, segment number <80 ..... *Bratislavia dadayi* (Michaelsen, 1905) [invasive in Europe, China. Nearctic. Neotropics]

2(1) Dorsal hair and needle chaetae both one (rarely two) per bundle; hair chaetae smooth, needle chaetae bifid with equally long, slightly diverging teeth; ventral chaetae 2−4 per bundle, teeth equally long in anterior and middle segments but the upper tooth slightly shorter in posterior ones; L = 2−4 mm ..... *Bratislavia prosetosa* (Liang, 1964) [China]

2′ Dorsal hair and needle chaetae both 1−3 per bundle; hair chaetae smooth, needle chaetae with two fine parallel teeth, the upper tooth slightly longer; in ventral bundles 2−7 chaetae, with teeth of equal length; in mature individuals penial chaetae by 4−6 per bundle, with two short teeth; L = 2−5 mm (Fig. 12.8(18−21)) ..... *Bratislavia palmeni* (Munsterhjelm, 1905) [western Palaearctic]

Oligochaeta: Tubificida: Naididae: Vejdovskyella: Species (excluding Lake Baikal)

1 Ventral chaetae absent in V, or also in IV, leaving a false impression that dorsal chaetae begin from V or IV (in fact, they begin from VI); hair chaetae thick and serrate, with two rows of rough denticles on its convex side; needle chaetae much thinner and simple-pointed; in mature individuals one single-pointed penial chaeta per bundle; eyes present (subgenus *Vejdovskyella*) 2

1′ Full set of ventral chaetae in II−V; hair chaetae mostly smooth (seldom finely serrate or pilose); no eyes (subgenus *Machetna*) 4

2(1) Ventral chaetae mostly with slightly longer upper tooth 3

2′ Ventral chaetae with twice longer upper tooth, in II−III by 2−4, from VI onwards mostly by three. Dorsal bundles consist of 3−4 hair chaetae and 3−4 much thinner, simple pointed needle chaetae. L = 1.1−2 mm, n = 9−12 ..... *Vejdovskyella* (*V.*) *simplex* Liang, 1958 [eastern Palaearctic]

3(2) Ordinary ventral chaetae by 1−3. In ventral bundles of VI, VII and sometimes also VIII, IX, single (rarely double) enlarged chaetae, strongly curved, with small upper tooth and very thick, curved lower tooth. Hair and needle chaetae altogether 4−12 per dorsal bundle. L = 1−3 mm ..... *Vejdovskyella* (*V.*) *macrochaeta* (Lastočkin, 1921) [eastern Europe, western Siberia]

3′ No enlarged ventral chaetae. All ventral chaetae similar, by 3−6. Hair chaetae 4−8 per bundle, needle chaetae by 1−8. L = 2−8 mm, n = 12−24 (Fig. 12.7(19−23)) ..... *Vejdovskyella* (*V.*) *comata* (Vejdovský, 1884) [Holarctic]

4(1) In VI (or also in some of the next segments) ventral chaetae thick and curved, with upper tooth split into 2−3 denticles. Ordinary ventral chaetae in II−V by 2−4, with slightly longer upper tooth; from VI onwards ventral chaetae singly. Dorsal bundles with 2−9 fine hair chaetae and 3−9 fine single-pointed needle chaetae. In mature individuals simple-pointed penial chaetae with simple hooked tip, one per bundle. No eyes. L = 1.3−3 mm, n = 11−14 (Fig. 12.7(24−28)) ..... *Vejdovskyella* (*Machetna*) *intermedia* (Bretscher, 1896) [western Palaearctic. Nearctic]

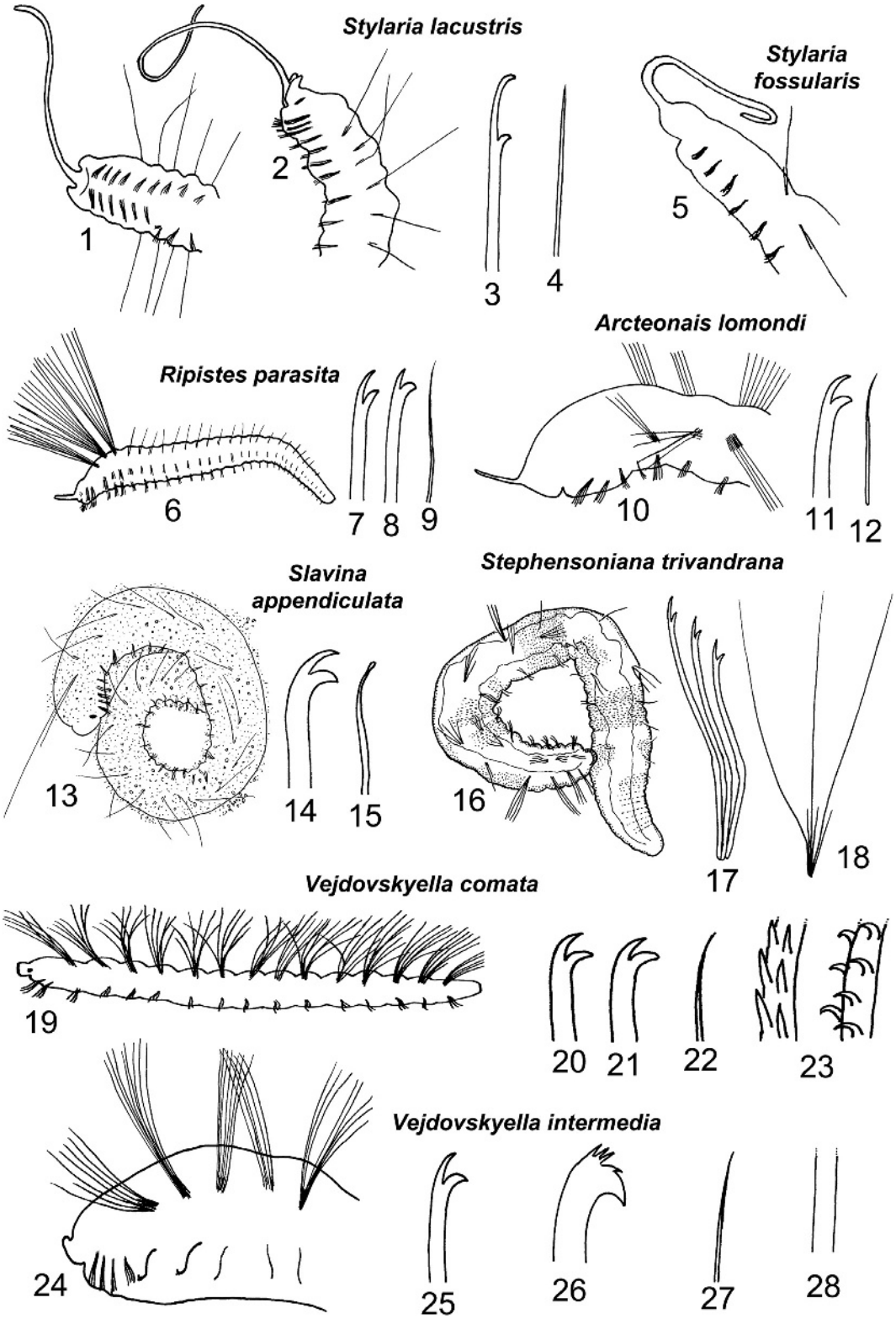


FIGURE 12.7 Naididae III: (1–4): *Stylaria lacustris*: (1) anterior end in ventral view, (2) anterior end in lateral view, (3) ventral chaeta, (4) needle chaeta; (5) *Stylaria fossularis*, anterior end; (6–9)*: Ripistes parasita*: (6) general view, (7) anterior ventral chaeta, (8) posterior ventral chaeta, (9) needle chaeta; (10–12): *Arcteonais lomondi*; (10) anterior end, (11) ventral chaeta, (12) needle chaeta; (13–15): *Slavina appendiculata*: (13) general view, (14) ventral chaeta, (15) needle chaeta; (16–18): *Stephensoniana trivandrana*: (16) general view, (17) ventral bundle, (18) dorsal bundle; (19–23): *Vejdovskyella comata*: (19) general view, (20) anterior ventral chaeta, (21) posterior ventral chaeta, (22) needle chaeta, (23) parts of hair chaetae; (24–28): *Vejdovskyella intermedia:* (24) anterior end, (25) ordinary ventral chaeta, (26) giant ventral chaeta, (27) needle chaeta, (28) part of a hair chaeta.

4′ Ventral chaetae in II−V three to four per bundle, further posterior 2−3, all similar in shape, with teeth of equal thickness but upper tooth 2−2.5 times longer; dorsal bundles consisting of thick, mucronate hair chaetae and thin simple pointed needle chaetae, both 1−2; mature individuals, 1−2 blunt pointed penial chaetae per bundle; prostomium very short, like a low cupola; no eyes; L = 0.7−3 mm ..... *Vejdovskyella* (*Machetna*) *koshovi* (Sokolskaja, 1962)
[Russia]

Oligochaeta: Tubificida: Naididae: *Allonais*: Species

1 Needle chaetae with two straight teeth without intermediate denticles 2

1′ Dorsal bundles with 1−2 hair chaetae and 1−2 needle chaetae with widely diverging teeth and 1−5 fine intermediate denticles. Ventral chaetae of II−V straighter and thinner than the rest, with slightly longer upper tooth; further backwards the teeth are equal or the upper one slightly shorter. In mature individuals hooked penial chaetae, obtuse or with vestigial upper tooth, 3−5 per bundle. (The posterior end with dorsally directed anus has been interpreted as a branchial disk with two pairs of small gills like in the genus *Dero*.) L = 1.5−8 mm (Fig. 12.8(22−26)) ..... *Allonais pectinata* (Stephenson, 1910)
[Palaearctic. Nearctic. Circumtropical]

2(1) Dorsal bundles beginning from V−VII, with 1−2 hair chaetae and 1−2 needle chaetae. Upper tooth of the needle chaetae much shorter, sometimes splitted or completely reduced. Ventral chaetae 2−8 per bundle, with equally long teeth; in anteriormost bundles shorter and with slightly longer teeth. Penial chaetae 3−11 per bundle, with simple hooked tip. Swimming. L = 4−60 mm ..... *Allonais paraguayensis* (Michaelsen, 1905)
[China. Circumtropical]

2′ Dorsal bundles beginning from VI, consisting of 1−2 hair chaetae and 1−2 needle chaetae. Needle chaetae with two straight, slightly diverging teeth of about equal length or the distal tooth slightly longer. Ventral chaetae in II−V 3−5 per bundle, with slightly longer upper tooth; in the following segments by 4−6, somewhat shorter, with teeth equally long. No modified penial chaetae. L = 2.5−3.5 mm ..... *Allonais gwaliorensis* (Stephenson, 1920)
[Turkey. Palaeotropical]

Oligochaeta: Tubificida: Naididae: *Nais*: Species (excluding Lake Baikal)

A separate key to the Naididae of Lake Baikal is given on p. 387.

1 Needle chaetae simple-pointed 2

1′ Needle chaetae bifid 8

2(1) Body not transversely striped; penial chaetae with obtuse, bent but not cochliform, sometimes with reduced upper tooth 3

2′ Body dorsal side with dark transverse stripes along the intersegmental furrows; dorsal bundles with 1−3 hair chaetae and 2−4 needle chaetae with simple apex; ventral chaetae in II−V 3−12 per bundle, in segments 4−15, often located in bundles in two rows; mature individuals with 5−8 penial chaetae per bundle, their tip cochliform, with concave side bearing a longitudinal keel; eyes very large; L = ∼20 mm ..... *Nais tygrina* Isossimov, 1962
[Russia: Lake Baikal and Angara River in Siberia]

3(2) Needle chaetae aciculate 4

3′ Needle chaetae apically blunt 6

4(3) Hair chaetae not serrate; body unpigmented 5

4′ Dorsal bundles with 1−3 thin serrate hair chaetae; hair chaetae < body diameter; 1−3 stout needle chaetae, almost straight but with apex slightly curved, simple; segment II ventral chaetae 4−6 per bundle, thin, with upper tooth 1.5−2 times longer, following segments ventral chaetae gradually shorter and thicker, with similar teeth; some individuals with dorsal bundles beginning on V instead of VI; body dorsally pigmented; L = 3−5 mm ..... *Nais baicalensis* Sokolskaja, 1962
[Russia: Lake Baikal and Angara River in Siberia]

5(4) Dorsal bundles with 1−5 thick, stiff, curved hair chaetae and 1−5 needle chaetae of the same shape, almost devoid of any nodulus; segments II−V ventral chaetae 2−5, with long almost parallel teeth, upper tooth considerably longer; segment VI on, ventral chaetae much thicker and more curved, with lower tooth longer and 2−3 times as thick as the upper; L = 3.5−6.5 mm, n = 11−19 (Fig. 12.8(27−30)) ..... *Nais barbata* Müller, 1774
[Holarctic. Australian and Oriental regions]

5′ Dorsal bundles with 1−3 straight hair chaetae and 1−3 needle chaetae bearing distinct nodulus; ventral chaetae 2−5, always with upper tooth thinner and up to 1.5 times as long as lower, from segment VI on slightly thicker; L = 1.5−6 mm, n = 11−18 (Fig. 12.8(31−34)) ..... *Nais pseudobtusa* Piguet, 1906
[Holarctic. Afrotropical, Australia, neotropical]

6(3) Segments II−V ventral chaetae teeth subparallel, diverging distally at an acute angle; needle chaetae nodulus at $^{1}/_{5}$−¼ from distal end 7

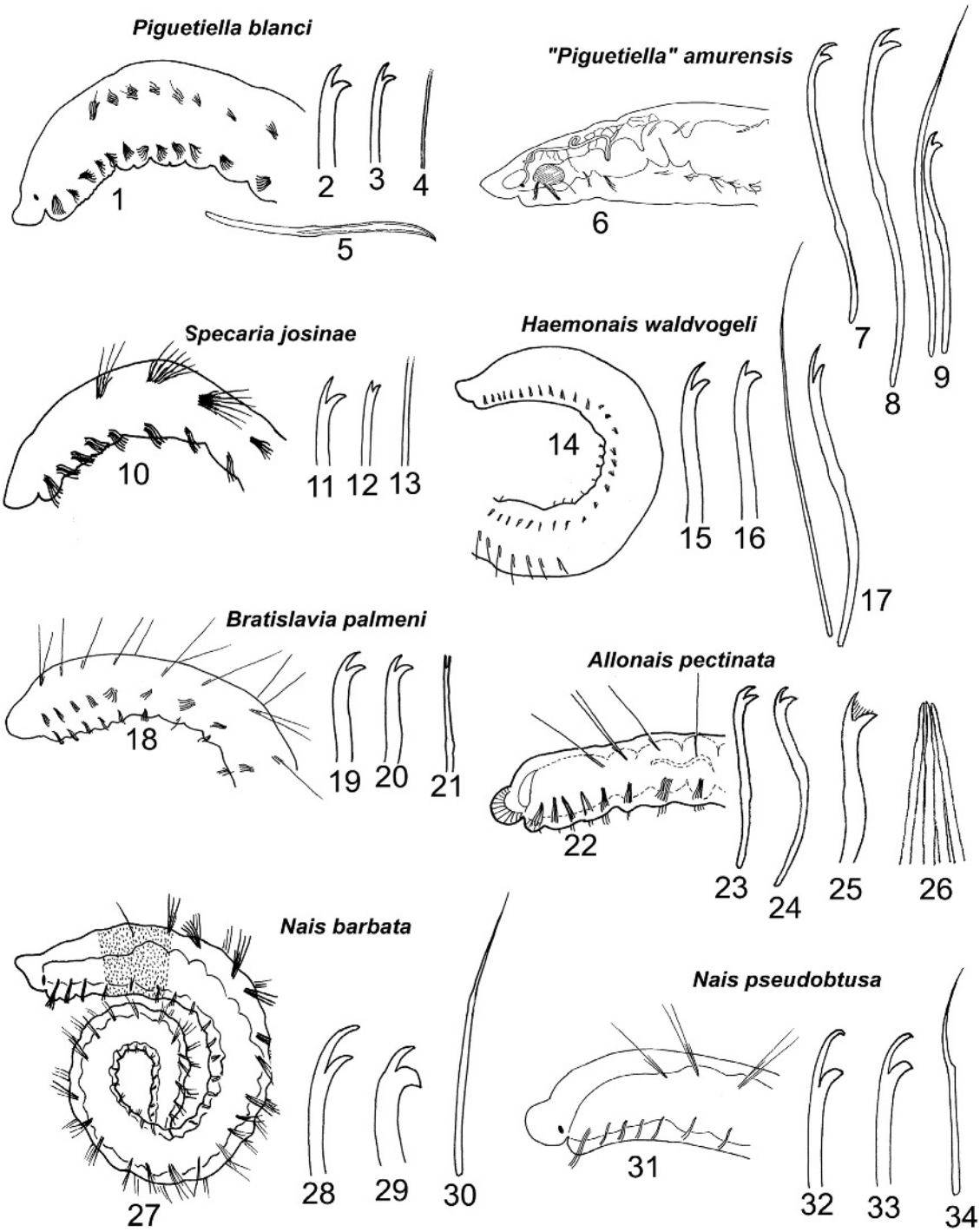


FIGURE 12.8 Naididae IV: (1–5): *Piguetiella blanci*: (1) anterior end, (2) ventral chaeta, (3) "needle" chaeta, (4) part of a hair chaeta, (5) spermathecal chaeta; (6–9): "*Piguetiella*" *amurensis*; (6) anterior end, (7) anterior ventral chaeta, (8) posterior ventral chaeta, (9) dorsal bundle; (10–13): *Specaria josinae*: (10) anterior end, (11) ventral chaeta, (12) "needle" chaeta, (13) part of a hair chaeta; (14–17): *Haemonais waldvogeli*: (14) anterior end, (15) anterior ventral chaeta, (16) posterior ventral chaeta, (17) dorsal bundle; (18–21): *Bratislavia palmeni*: (18) anterior end, (19) anterior ventral chaeta, (20) posterior ventral chaeta, (21) needle chaeta; (22–26): *Allonais pectinata*: (22) anterior end, (23) anterior ventral chaeta, (24) posterior ventral chaeta, (25) pectinate chaeta, (26) penial bundle; (27–30): *Nais barbata*: (27) general view of a sexually mature specimen with clitellum, (28) anterior ventral chaeta, (29) posterior ventral chaeta, (30) needle chaeta; (31–34): *Nais pseudobtusa*: (31) anterior end, (32) anterior ventral chaeta, (33) posterior ventral chaeta, (34) needle chaeta.

6′ Segments II−V ventral chaetae 2−5 per bundle, with teeth subequally thick, with upper one 1.6−2 times as long as lower; lower tooth diverging distally from upper (and from chaeta axis) almost at right angle; segment VI on ventral chaetae 2−5, shorter, thicker and more curved, with teeth subequally long; dorsal bundles with 1−2 hair and 1−2 apically blunt (seldom with rudimentary teeth) needle chaetae; in the needle chaetae nodulus at about $^{1}/_{3}$ from distal end; L = 4−9 mm, n = 14−22 (Fig. 12.9(1−3)) ..... *Nais simplex* Piguet, 1906
[cosmopolitan]

7(6) Segments II−V ventral chaetae 4−10, long and slender, with upper tooth very long, falciform; lower tooth much shorter, sometimes reduced, clinging to upper; segments VI on ventral chaetae 2−7 shorter and thicker, upper tooth twice as long as lower, but equally thick; dorsal bundles with one hair chaeta and 1−2 blunt needle chaetae; L = 3−5 mm, n ≤ 28 (Fig. 12.9(4−7)) ..... *Nais behningi* Michaelsen, 1923
[Holarctic]

7′ Segments II−V ventral chaetae 2−8, long and slender, with teeth subequally thick but upper tooth twice as long; segment VI on ventral chaetae 3−7, thicker; dorsal bundles of 1−2 hair chaetae and 1−2 blunt needle chaetae; L = 3.6−4.8 mm, n = 14−19 (Fig. 12.9(8−10)) ..... *Nais alpina* Sperber, 1948
[western Palaearctic. Nearctic]

8(1) Segments VI or VII on, some ventral bundles with thick giant chaetae with prolonged upper tooth; ventral chaetae in II−V with long parallel teeth 9

8′ No giant chaetae in any ventral bundles; segments II−V chaetae variable 11

9(8) Segment VI on, without any significant difference between VI and VII; lower tooth short but never cleft or reduced 10

9′ Segment VII on with giant chaetae, sometimes present to XIII, 1−2 per bundle, straight and extremely thick, with very short, cleft or reduced, lower tooth; II−V ventral chaetae 2−7, VI one, upper tooth twice as long as lower; VII and some subsequent segments with single giant chaetae, further ventral chaetae 2−5, thicker and more curved than anterior ones, with upper tooth twice as long; hair chaetae one, short; needle chaetae 1−2, with long parallel teeth; L = 3−7 mm, n = 13−22 (Fig. 12.9(11−16)) ..... *Nais bretscheri* Michaelsen, 1899
[Holarctic. Neotropics(?)]

10(9) Segments II−V, ventral chaetae 3−5, upper tooth twice as long; VI on, 2−3 enlarged ventral chaetae per bundle (the largest usually in VIII), thicker than anterior ones, with upper tooth up to four times longer; in about X their number increases to 4−5 while length decreases, and the ratio of two teeth length decreases to two again; hair and needle chaetae by one, needle chaetae with long parallel teeth; L = ? (Fig. 12.9(23−27)) ..... *Nais stolci* Hrabě, 1981
[western Palaearctic. Nearctic]

10′ Segments II−V, ventral chaetae 2−5, upper tooth 1.5−2 times as long; segment VI on, ventral chaetae usually ordinary, 2−5 per bundle, thicker and more curved, with teeth equally long or upper tooth slightly longer and thinner; often VI and in some subsequent segments single giant chaetae per bundle, thicker and with upper tooth 2−3 times as long as lower; hair chaetae < body diameter, 1−2; needle chaetae 1−2, with short but distinct teeth; segment VIII, esophagus to wide midgut ("stomach") abrupt transition, long cells projecting as brown appendages into cavity; L = 2.5−9 mm, n = 13−21 (Fig. 12.9(17−22)) ..... *Nais pardalis* Piguet, 1906 (in part)
[Holarctic. Neotropic. Oriental]

11(8) Needle chaetae long and parallel 12

11′ Needle chaetae teeth short, sometimes hardly recognizable 13

12(11) Dorsal bundles consisting of 1−4 hair chaetae and 1−4 needle chaetae, the latter with fine but relatively long parallel teeth; ventral chaetae uniform, 2−5 per bundle, with upper tooth twice as long and strongly curved distally, lower tooth forming a right angle with chaeta longitudinal axis; L = 2.2−12 mm, n = 12−21; springs, heavily polluted streams, and brackish water ..... *Nais elinguis* Müller, 1774
[cosmopolitan]

12′ Dorsal bundles consisting of 1−2 faintly serrate hair chaetae and 1−2 needle chaetae, the latter with fine but extremely long (∼20 times longer than thick) parallel teeth; ventral chaetae 3−5, in II−V slightly longer than in subsequent segments, all with somewhat longer upper tooth; posterior ones with small intermediate denticles; L = 3−8 mm, segment number 34−41 ..... *Nais longidentata* Cui, He, Peng & Wang, 2015
[China: Tibet]

13(11) Segments II−V ventral chaetae teeth subparallel, diverging distally at an acute angle 14

13′ Segments II−V ventral chaetae lower tooth distal end diverging from upper tooth (and chaeta longitudinal axis) almost at right angle 15

14(13) Dorsal hair and needle chaetae 1−2 per bundle; hair chaetae long, needle chaetae finely bifid; segments II−V ventral chaetae with equally thin teeth but the upper tooth 1.5−2 times as long; VI on, ventral chaetae much thicker and more curved, with lower tooth several times thicker; mature individuals hooked penial chaetae 2−3; intestine beginning without long, projecting cells; L = 5−8 mm, n = 16−23 (Fig. 12.9(44−46)) ..... *Nais christinae* Kasprzak, 1973
[Europe]

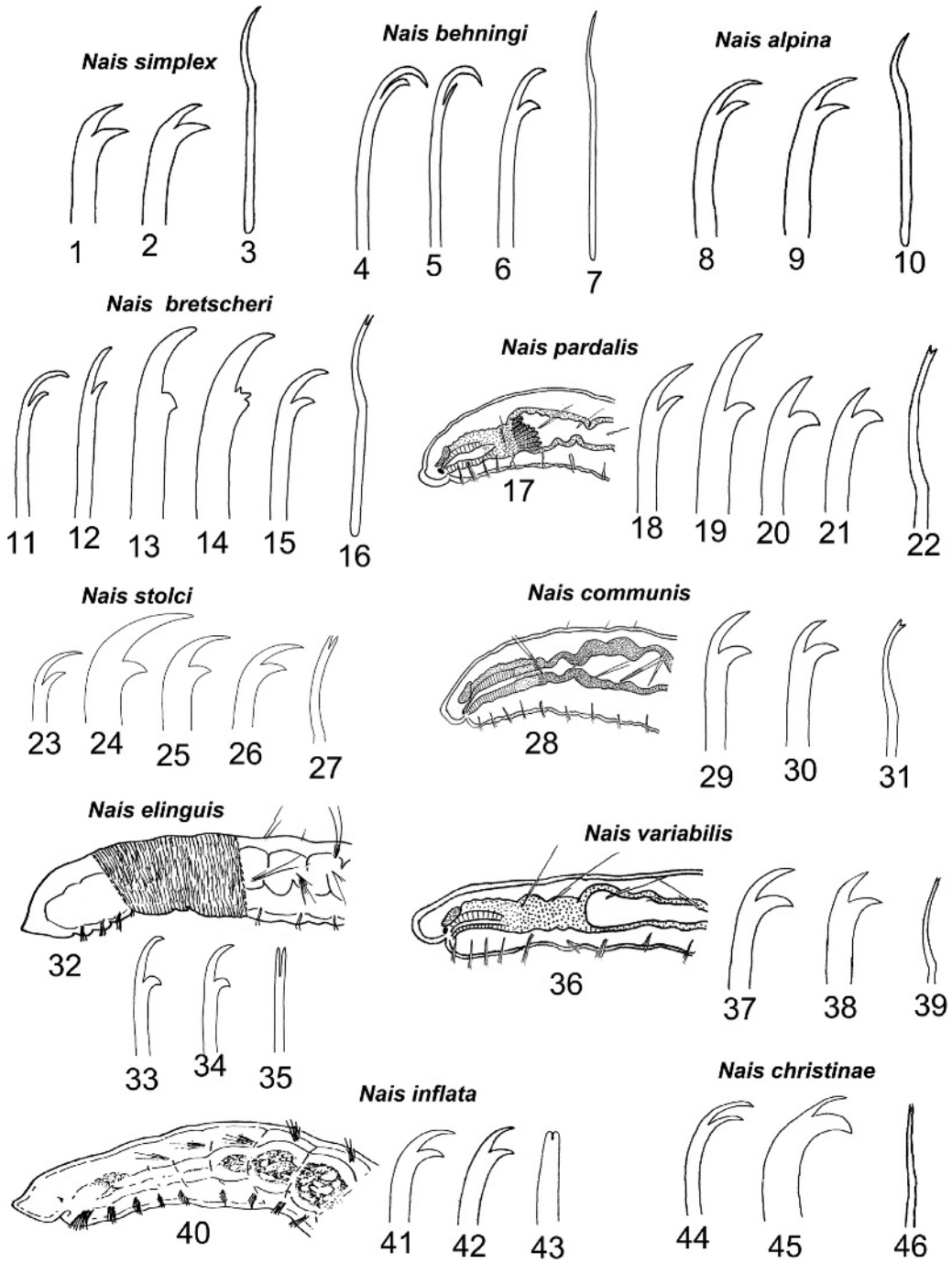


FIGURE 12.9 Naididae V: (1–3): *Nais simplex*: (1) anterior ventral chaeta, (2) posterior ventral chaeta, (3) needle chaeta; (4–7): *Nais behningi*; (4, 5) anterior ventral chaetae, (6) posterior ventral chaeta, (7) needle chaeta; (8–10): *Nais alpina*: (8) anterior ventral chaeta, (9) posterior ventral chaeta, (10) needle chaeta; (11–16): *Nais bretscheri*: (11) anterior ventral chaeta, (12) ventral chaeta of VI, (13, 14) giant ventral chaetae beginning from VII, (15) posterior ventral chaeta, (16) needle chaeta; (17–22): *Nais pardalis*: (17) anterior end with beginning of intestine, (18) anterior ventral chaeta, (19) giant ventral chaeta beginning from VI, (20, 21) posterior ventral chaetae, (22) needle chaeta; (23–27): *Nais stolci*: (23) anterior ventral chaeta, (24) giant ventral chaeta beginning from VI, (25. 26) gradually diminishing posterior ventral chaetae, (27) needle chaeta; (28–31): *Nais communis*: (28) anterior end with beginning of intestine, (29) anterior ventral chaeta, (30) posterior ventral chaeta, (31) needle chaeta; (32–35): *Nais elinguis*: (32) anterior end of sexually mature specimen with clitellum, (33) anterior ventral chaeta, (34) posterior ventral chaeta, (35) needle chaeta; (36–39): *Nais variabilis*: (36) anterior end with beginning of intestine, (37) anterior ventral chaeta, (38) posterior ventral chaeta, (39) needle chaeta; (40–43): *Nais inflata*: (40) anterior end, (41) anterior ventral chaeta, (42) posterior ventral chaeta, (43) needle chaeta; (44–46): *Nais christinae*: (44) anterior ventral chaeta, (45) posterior ventral chaeta, (46) needle chaeta.

14′ Hair chaetae shorter than body diameter, 1−2; needle chaetae 1−2, with short but distinct teeth; II−V ventral chaetae 2−5, upper tooth 1.5−2 times as long; VI on, ventral chaetae 2−5 per bundle, thicker and more curved, with teeth equally long or upper tooth slightly longer and thinner; often VI and some subsequent segments with single giant chaetae per bundle, thicker and with upper tooth 2−3 times longer than lower; in mature individuals hooked, simple penial chaetae three; segment VIII esophagus to the wide midgut ("stomach") abrupt transition, long cells projecting as brown appendages into cavity; L = 2.5−9 mm, n = 13−21 (Fig. 12.9(17−22)) ..... *Nais pardalis* Piguet, 1906 (in part) [Holarctic. Neotropic. Oriental]

15(13) Spermathecal ducts terminating with a penis-like protrusion included in a spacious pouch; mostly in brackish water of the North Pacific region 16

15′ Spermathecal ducts opening immediately on the body surface; freshwater 17

16(15) Hair chaetae 0−2, thin, < body diameter; needle chaetae 1−2, sigmoid, with distinct sharp teeth, upper somewhat thinner than lower; ventral chaetae uniform, 1.5−2 times > upper tooth but in II−V somewhat straighter, 4−5 per bundle, beginning from VI 3−4; L = 3−8 mm, n = 18; brackish water lakes and marine littoral ..... *Nais borutzkii* Sokolskaja, 1964 [Russia: Pacific coast]

16′ Hair chaetae 0−3 per bundle, curved and blunt-tipped, only 1.2−1.4 times as long as needle chaetae; needle chaetae 1−3, with relatively large teeth diverging at sharp angle; ventral chaetae uniform with slightly thinner and longer upper tooth, somewhat longer in II−V, 3−5; L = 4−8 mm, n = 16−26; slightly brackish coastal lakes ..... *Nais kisui* Sato, Ohtaka & Timm, 2009 [Japan]

17(15) Esophagus abruptly dilating into midgut; needle chaetae with tiny, sometimes hardly visible teeth; able to swim 18

17′ Esophagus gradually dilating into midgut; hair and needle chaetae 1−2 per bundle; needle chaetae with distinctly diverging teeth; II−V ventral chaetae 2−7, with upper tooth longer and thinner; VI on 2−6, slightly thicker and more curved, with gradually leveling tooth length; not swimming; L = 1.5−12 mm, n = 10−21 (Fig. 12.9(28−31)) ..... *Nais communis* Piguet, 1906 [cosmopolitan]

18(17) Hair chaetae ≤three per bundle, relatively long; needle chaetae teeth sharp; smaller worms 19

18′ Hair chaetae 0−5 (typically three to four) per bundle, less than twice as long as needle chaetae, very finely pilose in SEM; needle chaetae stout, with short, blunt teeth; ventral chaetae uniform, with teeth of equal thickness, upper tooth longer; II with 5−8 per bundle, subsequent segments 2−5; relatively large and stout; L = 3.2−4.3 mm, n = 18−19 (Fig. 12.9(40−43)) ..... *Nais inflata* Liang, 1963 [China]

19(18) Hair and needle chaetae 1−2 per bundle; ventral chaetae 2−7, longer in II−V, with upper tooth longer and thinner; VI on, shorter, often thicker and more curved, with subequal teeth or upper tooth slightly longer but thinner; L = 4−10 mm, n = 12−21 (Fig. 12.9(36−39)) ..... *Nais variabilis* Piguet, 1906 [nearly cosmopolitan]

19′ Hair chaetae two per bundle, needle chaetae two (seldom 3−4); II−V ventral chaetae 5−6 (seldom to eight) per bundle, longer and straighter, the upper tooth 1.5−2 times > than lower; VI on 4−5, shorter and thicker, tooth length decreasing to 1.2−1.5; posteriormost chaetae can have subequal teeth; L = 1.9−5.1 mm, n = 15−30 ..... *Nais bekmanae* Sokolskaja, 1962 [Russia: Lake Baikal and Angara River in Siberia]

Oligochaeta: Tubificida: Naididae: Genera (Lake Baikal)

This key is modified after Semernoy (2004).

1 Dorsal chaetae present in at least some posterior segments; ventral chaetae present in III−V; prostomium well developed 2

1′ Dorsal chaetae lacking; first five segments fused, bearing a single pair of ventral bundles (II), the next bundles appearing only in VI; prostomium more or less reduced, mouth terminal, pharynx cylindrical and thick, followed by a large stomach; mature individuals with male pores and penial chaetae in VI ..... ***Chaetogaster*** **[p. 388]**

2(1) Dorsal bundles from VI 3

2′ Dorsal bundles from III ..... ***Amphichaeta*** **[p. 390]**

3(2) No hair chaetae 4

3′ Hair chaetae present in dorsal bundles 6

4(3) Dorsal bundles with several bifid, not peg-like chaetae 5

4′ Dorsal bundles, from VI (sometimes backwards), single thick, peg-like chaetae with bluntly simple or bifid tip; ventral bundles with ordinary bifid chaetae; mature individuals VI with blunt, curved penial chaetae, 2−3 per bundle; elongate body; dark transverse pigment stripes may occur on anteriormost segments; eyes present; L = 6−36 mm, n = 23−51 (Fig. 12.6(3−5)) ..... *Ophidonais serpentina* (Müller, 1774) [Holarctic. Neotropics]

5(4) Both dorsal and ventral bundles with uniform bifid chaetae ..... ***Uncinais*** **[p. 391]**

5′ II–V ventral chaetae 5–7 per bundle, with simple, strongly curved distal ends; other segments both ventral and dorsal chaetae 2–7 per bundle, bifid, with upper tooth slightly shorter; L = 4–6 mm, n = 20–40 (Fig. 12.10(37–39)) ..... *Neonais elegans* Sokolskaja, 1962 [Lake Baikal]

6(3) Prostomium with tentacle 7

6′ No tentacle on prostomium 8

7(6) VI–VIII, dorsal bundles of 2–16 extremely long hair chaetae with numerous shorter hair chaetae and fine acute needle chaetae; IX on, shorter hair chaetae and needle chaetae, both 1–3 per bundle; II–III ventral bundles with 2–7 chaetae with longer upper tooth; IV–V, no ventral chaetae; VI on, 3–8, with shorter upper tooth; swimming, sometimes constructing tubes attached to water plants; L = 2–7.5 mm, n = 14–21 (Fig. 12.7(6–9)) ..... *Ripistes parasita* (Schmidt, 1847) [Holarctic]

7′ VI–VIII without prolonged chaetae; tentacle several times longer than body diameter; hair and simple needle chaetae numerous, relatively thick, stiff; ventral chaetae with two seemingly broken portions proximally, with upper tooth much longer and strongly curved distally ..... ***Stylaria* [p. 391]**

8(6) Body surface smooth 9

8′ Body armored with foreign matter adhering to cutaneous glands; dorsal bundles of thin hair and needle chaetae, both 1–2; VI hair chaetae considerably longer than on subsequent segments; needle chaetae with a small knob apically; ventral chaetae 2–5, all with slightly longer and thinner upper tooth; eyes present; not swimming; L = 2–20 mm, n = 19–29 (Fig. 12.7(13–15)) ..... *Slavina appendiculata* (Udekem, 1855) [cosmopolitan]

9(8) Hair chaetae long and flexible, needle chaetae simple pointed or bifid; eyes (mostly) present, more seldom lacking 10

9′ Hair chaetae stiff, mucronate, accompanied with thinner, simple needle chaetae; no eyes ..... ***Vejdovskyella* [p. 391]**

10(9) Dorsal bundles with 2–6 sigmoid crotchets, finer and straighter than ventral ones, with short equal teeth, together with 2–6 hair chaetae; ventral chaetae 5–10, with slightly longer upper tooth, similar in anterior and posterior; no eyes; L = 3–10 mm, n = 11–27 ..... *Specaria josinae* (Vejdovský, 1884) [Holarctic]

10′ Dorsal bundle needle chaetae much thinner and straighter than ventral crochets, with simple or bifid apex; eyes present ..... ***Nais* [p. 392]**

Oligochaeta: Tubificida: Naididae: *Chaetogaster*: Species (Lake Baikal)

1 Free-living 2

1′ Epibionts of gastropods; chaetae uniform, with strongly curved subequal teeth, or with upper tooth shorter; II with 5–20 chaetae per bundle, 53–123 μm long, posterior segments with 4–20, shorter; L = 0.7–5 mm, n = 8–9 (Fig. 12.5(8–9)) ..... *Chaetogaster limnaei* Baer, 1827 [cosmopolitan]

2(1) All chaetae bifid 3

2′ At least some chaetae simple 10

3(2) Chaetae uniform 4

3′ Chaetae all bifid but different within a bundle or in different bundles 9

4(3) II chaetae larger than the rest 5

4′ Chaetae of all bundles of similar size 7

5(4) Prostomium reduced 6

5′ Prostomium well developed; pharynx with chitinoid lining; all chaetae with thinner, shorter upper tooth, in II 52 μm long; L = 0.45 mm, n = 8–9; littoral (Fig. 12.10(1–2)) ..... *Chaetogaster crocodilus* Semernoy, 1985 [Lake Baikal]

6(5) Mouth dorsal edge notched; II chaetae 8–11 per bundle, 147–255 μm long, with upper tooth twice as long as lower; VI on, seven chaetae per bundle, shorter; L = 2.5–25 mm, n = 9–12 (Fig. 12.5(1–4)) ..... *Chaetogaster diaphanus diaphanus* (Gruithuisen, 1828) [cosmopolitan]

6′ Mouth dorsal edge not notched; II up to seven chaetae, 130–153 μm long, with twice as long upper tooth; VI on, chaetae by 8–9, shorter; littoral ..... *Chaetogaster diaphanus litoralis* Semernoy, 1985 [Lake Baikal]

7(4) Chaetae with longer upper tooth 8

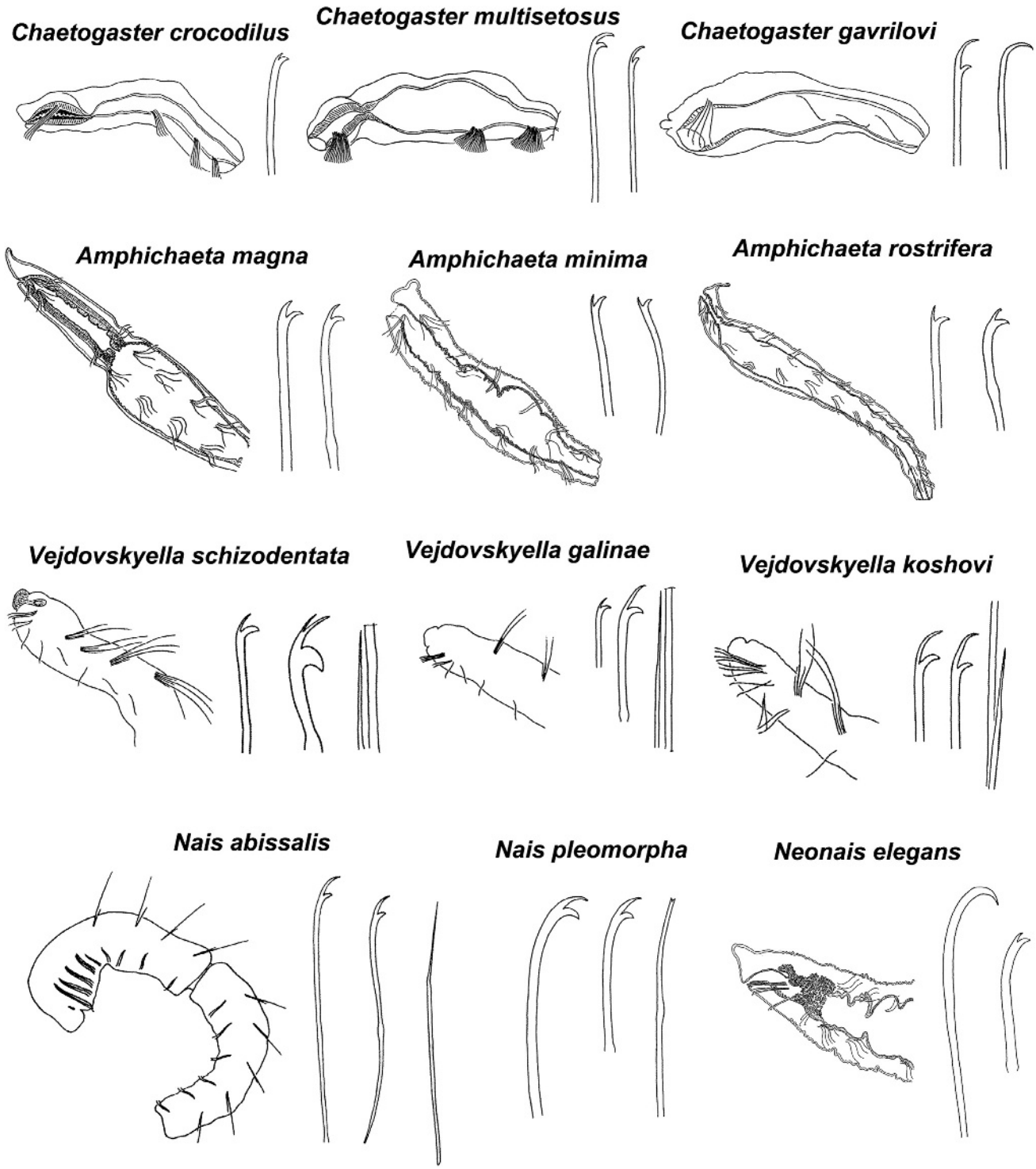


FIGURE 12.10 Naididae from Lake Baikal: (1, 2) *Chaetogaster crocodilus*: (1) first zooid, (2) chaeta; (3–5): *Chaetogaster multisetosus*: (3) first zooid, (4) chaeta of II, (5) posterior chaeta; (6–8): *Chaetogaster gavrilovi*: (6) first zooid, (7) chaeta of II, (8) posterior chaeta; (9–11): *Amphichaeta magna*: (9) anterior end, (10) anterior chaeta, (11) posterior chaeta; (12–14): *Amphichaeta minima*: (12) first zooid, (13) anterior chaeta, (14) posterior chaeta; (15–17): *Amphichaeta rostrifera*: (15) general view, (16) anterior chaeta, (17) posterior chaeta; (18–21): *Vejdovskyella schizodentata*: (18) anterior end, (19) anterior ventral chaeta, (20) posterior ventral chaeta, (21) needle chaeta and fragment of hair chaeta; (22–25): *Vejdovskyella galinae*: (22) anterior end, (23) anterior ventral chaeta, (24) posterior ventral chaeta, (25) needle chaeta and fragment of hair chaeta; (26–29): *Vejdovskyella koshovi*: (26) anterior end, (27) anterior ventral chaeta, (28) posterior ventral chaeta, (29) needle chaeta and fragment of hair chaeta; (30–33): *Nais abissalis*: (30) chain of two zooids, (31) anterior ventral chaeta, (32) posterior ventral chaeta, (33) needle chaeta; (34–36): *Nais pleomorpha*: (34) anterior ventral chaeta, (35) posterior ventral chaeta, (36) needle chaeta; (37–39): *Neonais elegans*: (37) anterior end, (38) anterior ventral chaeta, (39) posterior chaeta.

7′ Chaetae with teeth of equal length, 6−9 per bundle, those of II 130−177 μm long; L = 0.85 mm, n = 8−13; littoral ..... *Chaetogaster ignotus* Semernoy, 1985
[Lake Baikal]

8(7) All chaetae upper tooth 2.5 times > than lower; II up to 10 per bundle, 177 μm long; VI−VIII chaetae 20−22; L = 0.5−1.2 mm, n = 8 (Fig. 12.10(3−5)) ..... *Chaetogaster multisetosus* Semernoy, 1985
[Lake Baikal]

8′ All chaetae upper tooth 1.5−2 times > lower; chaetae of II longest and thickest, 177−187 μm long, 8−10 per bundle, with upper tooth 1.5 times > lower; VI on, 6−8, with upper tooth twice as long; chaetae hollow; segments II−V forming half the body length; L = 1.2 mm, n = 6−8 ..... *Chaetogaster cannibalus* Semernoy, 1985
[Lake Baikal]

9(3) All bundles with ordinary chaetae and one thicker and shorter chaeta; II ordinary chaetae 5−6, 77−118 μm long; VI on, 6−8, slightly shorter; L = 0.42−0.8 mm, n = 7 ..... *Chaetogaster grandisetosus* Semernoy, 1985
[Lake Baikal]

9′ II chaetae with upper tooth 1.5 times > than lower, 12−14 per bundle, 147−177 μm long; VI on, chaetae with rudimentary lower tooth, 8−9 per bundle, shorter; L = 0.65−1.1 mm, n = 8 ..... *Chaetogaster paucus* Semernoy, 1985
[Lake Baikal]

10(2) Chaetae of two types 11

10′ Chaetae of three types; II with 5−6 simple, sigmoid chaetae per bundle, 88−124 μm long, combined with one shorter, thicker and straighter chaeta; VI on, chaetae four per bundle, with rudimentary lower tooth; prostomium rudimentary; L = 0.5−0.8 mm ..... *Chaetogaster intermedius* Akinschina, 1984
[Lake Baikal and Angara River in Siberia]

11(10) II with seven simple-pointed chaetae, 106−142 μm long; VI on, bifid chaetae, 6−7, shorter, with rudimentary lower tooth; prostomium rudimentary; L = 0.65−0.83 mm, n = 9 ..... *Chaetogaster dissetosus* Semernoy, 1985
[Lake Baikal]

11′ II with four bifid chaetae, 65−72 μm long, with upper tooth four times > than lower; VI on, 1−2 strongly hooked simple-pointed chaetae; prostomium developed as three suboval papillae; L = 0.6 mm, n = 9 (Fig. 12.10(6−8)) ..... *Chaetogaster gavrilovi* Semernoy, 1985
[Lake Baikal]

Oligochaeta: Tubificida: Naididae: *Amphichaeta*: *S*pecies (Lake Baikal)

1 Prostomium without tentacle 2

1′ Prostomium with a thin tentacle; III dorsal chaetae and II−III ventral chaetae three per bundle; IV−V chaetae two, posterior 2−3; L = 0.8−1.2 mm (Fig. 12.10(15−17)) ..... *Amphichaeta rostrifera* Akinschina, 1984
[Lake Baikal and Angara River in Siberia]

2(1) Chaetae with nodulus 3

2′ Chaetae without nodulus, very thin 10

3(2) Pharynx lined with thickened cuticle 4

3′ Cuticular lining of pharynx not thickened 5

4(3) Pharyngeal musculature very thick, fused with the body wall; prostomium either oval or prolonged; II ventral chaetae four to seven, III 4−6 per bundle, with shorter upper tooth; following segments chaetae 3−4, with teeth equally long or the upper tooth longer; L = 2.3−5 mm (Fig. 12.10(9−11)) ..... *Amphichaeta magna* Sokolskaja, 1962
[Lake Baikal and Angara River in Siberia]

4′ Pharyngeal musculature not very thick, not fused with body wall; prostomium short and broad; II ventral chaetae 5−6, III chaetae 4−6 per bundle, with much shorter upper tooth; following segment chaetae 3−4, thinner than the former, with subequal teeth; L = = 1.0 mm ..... *Amphichaeta distincta* Semernoy, 2004
[Lake Baikal]

5(3) Mouth segment (I) distinct; pharynx with thick muscular walls 6

5′ Mouth segment (I) rudimentary; pharynx with thin walls and wide lumen; chaetae long and sigmoid, with slightly shorter upper tooth; II−III ventral chaetae 3−4 per bundle; III dorsal chaetae seven; II−III chaetae widened distally; IV−V chaetae two; following segments 3−4; prostomium rounded ..... *Amphichaeta nikae* Semernoy, 2004
[Lake Baikal and Angara River in Siberia]

6(5) Mouth segment (I) lined with thickened epithelium 7

6′ Mouth epithelium not thickened 9

7(6) Thickened mouth epithelium forming a "lower lip" 8

7′ Thickened mouth epithelium not protruded as "lower lip"; chaetae short and thick, anterior chaetae relatively straight, the posterior ones sigmoid; II ventral chaetae 3−5 per bundle, with shorter upper tooth; III chaetae 3−5; IV−V chaetae two; following segments three, the teeth length becoming gradually equal or upper tooth slightly longer; prostomium either triangular or broad and oval; L = 0.9−1.1 mm ..... *Amphichaeta annae* Semernoy, 2004
[Lake Baikal and Angara River in Siberia]

8(7) Pharyngeal musculature very thick, fused with the body wall musculature 9

8′ Pharynx musculature filling most of II−III but not fused to body wall; II ventral chaetae 5−8 per bundle; III chaetae 7−8, with much thinner and shorter upper tooth; IV−V chaetae 2−3; posteriors segments 2−5, teeth length becoming gradually equal; prostomium broad, suboval; L = 1.9−2.1 mm ..... *Amphichaeta labialia* Semernoy, 2004
[Lake Baikal]

9(8) Body wall cuticle and longitudinal musculature thin; III ventral chaetae 8−9 per bundle, III chaetae 5−6, with shorter upper tooth; following segments 2−4, teeth becoming gradually equal or the upper tooth slightly longer; L = 1.7 mm ..... *Amphichaeta aliena* Semernoy, 2004
[Lake Baikal]

9′ Body wall cuticle and longitudinal musculature thick; II ventral chaetae eight to nine per bundle, with slightly shorter upper tooth; III chaetae seven; following segments 2−5, with almost equally long teeth; L = 3.0 mm ..... *Amphichaeta altera* Semernoy, 2004
[Lake Baikal]

10(2) Mouth segment (I) with well-developed "under lip" epithelium; pharynx with thick musculature; II ventral chaetae 5−7; III chaetae six, with about equally long teeth; IV−V chaetae 3−4; following segments 3−5, the upper tooth slightly longer; L = 0.6−1.4 mm ..... *Amphichaeta nana* Semernoy, 2004
[Lake Baikal]

10′ Mouth segment (I) short, poorly defined; pharynx with thin musculature and wide lumen; II ventral chaetae four per bundle; III chaetae 4−5; following segments 3−4, all with upper tooth shorter and thinner than lower; L = 0.6 mm (Fig. 12.10(12−14)) ..... *Amphichaeta minima* Semernoy, 2004
[Lake Baikal]

Oligochaeta: Tubificida: Naididae: Uncinais: Species (Lake Baikal)

1 All chaetae with upper tooth slightly longer (the length decreasing posteriorly); II ventral bundles with 2−7 chaetae; following segments 2−4; mature individuals VI male pores with 2−3 blunt-tipped penial chaetae; forebody may have dorsal pigment spots; L = 5−18 mm, n = 19−27 (Fig. 12.6(1−2)) ..... *Uncinais uncinata* (Oersted, 1842)
[Palaearctic. Nearctic. Neotropics]

1′ Chaetae with equal teeth or, in posterior segments, with slightly shorter upper tooth; mature individual VI male pores 3−4 blunt-tipped penial chaetae; L = 2.8−5 mm ..... *Uncinais minor* Sokolskaja, 1962
[Lake Baikal and Angara River in Siberia]

Oligochaeta: Tubificida: Naididae: *Stylaria*: Species (Lake Baikal)

1 Prostomium with short protuding lobe on either side of tentacle; dorsal bundles with 1−3 hair and 3−4 needle chaetae; ventral chaetae 4−7; mature individual penial chaetae two, hooked; swims well; L = 5.5−18 mm, n = 15−35 (Fig. 12.7(1−4)) ..... *Stylaria lacustris* (Linnaeus, 1767)
[Holarctic. Neotropical. Afrotropical]

1′ Prostomium rounded, without protruding lobes; dorsal bundles usually with two hair and 1−3 needle chaetae; ventral chaetae 5−14; mature individual penial chaetae 2−3, hooked; L = 4−18 mm, n = 15−34 (Fig. 12.7(5)) ..... *Stylaria fossularis* Leidy, 1852
[eastern Palaearctic. Nearctic. Afrotropical. Australia]

Oligochaeta: Tubificida: Naididae: *Vejdovskyella*: Species (Lake Baikal)

1 Some ventral locomotory chaetae enlarged 2

1′ No enlarged ventral chaetae; VI ventral chaetae only slightly thicker than on II−V 6

2(1) Enlarged ventral chaetae with upper tooth cleft 3

2′ Enlarged ventral chaetae with simple upper tooth 4

3(2) Enlarged chaetae upper tooth with two small prongs, upper prong considerably thinner and shorter; II ventral chaetae three per bundle; III−V ventral chaetae one, with shorter upper tooth; VI−X enlarged chaetae one; XI and following with thin bifid chaetae; dorsal bundles

with 2−3 smooth(?) hair chaetae and three needle chaetae; L = 1 mm ..... *Vejdovskyella* (*Machetna*) *baicalensis* Semernoy, 1994
[Lake Baikal]

3′ Enlarged chaetae upper tooth long, cleft into 2−3 prongs; II ventral chaetae 3−4 per bundle; III with three; IV−V with one, with slightly shorter upper tooth; VI and following with enlarged chaetae with very strongly curved lower prong, one; dorsal bundles with serrate hair chaetae and needle chaetae, both by one to three; L = 2 mm (Fig. 12.10(18−21)) ..... *Vejdovskyella* (*Machetna*) *schizodentata* Semernoy, 1982
[Lake Baikal]

4(3) Enlarged chaetae with upper tooth length ≤ lower 5

4′ Enlarged chaetae with upper tooth twice as long and three times thinner than lower; II−III ventral chaetae 3−5 per bundle; IV−V ventral chaetae one, with teeth of equal length but upper tooth thinner; VI and following enlarged chaetae one, with upper tooth about twice as long as lower; dorsal bundles 2−3 smooth(?) hair chaetae and 3−4 needle chaetae; L = 1 mm; littoral (Fig. 12.10(22−25)) ..... *Vejdovskyella* (*Machetna*) *galinae* Semernoy, 1994
[Lake Baikal]

5(4) Enlarged chaetae with upper tooth shorter than the lower; II−III ventral chaetae 3−4 per bundle; IV−V two, with longer upper tooth; VI and following, enlarged chaetae one; dorsal bundle serrate hair chaetae and needle chaetae both three; L = 1.1 mm; at 50 m depth ..... *Vejdovskyella* (*Machetna*) *dilucida* (Snimschikova, 1987)
[Lake Baikal]

5′ Enlarged chaetae with upper tooth thin and as long as lower, erect; II ventral chaetae four per bundle; III three; IV−V two, with somewhat longer upper tooth; VI and following, enlarged chaetae one; dorsal bundle serrate hair chaetae and needle chaetae three; L = 1.1 mm; at 120 m depth ..... *Vejdovskyella* (*Machetna*) *sublitoralis* Semernoy, 1994
[Lake Baikal]

6(1) All ventral chaetae with equally thick teeth, upper teeth 2−2.5 times as long as lower; II ventral chaetae longest, four per bundle; III−V three; posterior segments 2−3; mature individual, penial chaetae 1−2, distally hooked; dorsal bundles smooth(?) hair chaetae and needle chaetae two; L = 0.7−3 mm (Fig. 12.10(26−29)) ..... *Vejdovskyella* (*Machetna*) *koshovi* (Sokolskaja, 1962)
[Lake Baikal and Angara River in Siberia]

6′ All ventral chaetae with teeth of equal length but upper tooth considerably thinner; II ventral chaetae four per bundle; III three; IV−V two; posterior segments one and slightly thicker; dorsal bundles one smooth(?) hair chaeta and one needle chaeta; L ≤ 3 mm ..... *Vejdovskyella* (*Machetna*) *margaritae* Semernoy, 1994
[Lake Baikal]

Oligochaeta: Tubificida: Naididae: *Nais*: Species (Lake Baikal)

1 Needle chaetae not considerably thicker than hair chaetae 2

1′ Dorsal bundles with 1−3 thin serrate hair chaetae shorter than body diameter, and 1−3 stout needle chaetae, almost straight but with slightly curved simple apex; II with 4−6 ventral chaetae per bundle, thin, with upper tooth 1.5−2 times longer than lower; following segments with ventral chaetae gradually shorter and thicker, with teeth similar; some individuals with dorsal bundles beginning in V instead of VI; dorsally pigmented; L = 3−5 mm ..... *Nais baicalensis* Sokolskaja, 1962
[Lake Baikal and Angara River in Siberia]

2(1) Needle chaetae with distinct nodulus 3

2′ Needle chaetae with elongated, acute tip, their nodulus indistinct 14

3(2) No dorsal transverse pigmented stripes 4

3′ Dorsally with dark transverse stripes along intersegmental furrows; dorsal bundles with 1−3 hair chaetae and 2−4 needle chaetae simple-pointed, thin; II−V ventral chaetae 3−12 per bundle, in following segments 4−15, bundles often in two rows; mature individuals 5−8 penial chaetae per bundle, the apex spatulate, concave side with longitudinal keel; eyes very large; L = ∼20 mm ..... *Nais tygrina* Isossimov, 1962
[Lake Baikal and Angara River in Siberia]

4(3) Needle chaetae simple-pointed 5

4′ Needle chaetae bifid 8

5(4) Hair chaetae thick and stiff 6

5′ Hair chaetae thin and flexible 7

6(5) Dorsal bundles with 1−5 curved, smooth hair chaetae < three times as long as needle chaetae, 1−5 needle chaetae of same shape, nodulus obscured; II−V ventral chaetae 2−5, with long almost parallel teeth, upper tooth being considerably longer; VI and following with ventral chaetae much thicker and more curved, lower tooth longer and 2−3 times as thick as the upper; L= 3.5−6.5 mm, n = 11−19 (Fig. 12.8(27−30)) ..... *Nais barbata* Müller, 1774
[Holarctic. Australian and Oriental regions]

6′ Dorsal hair chaetae finely serrate, up to twice as long as needle chaetae; both hair and needle chaetae 4−5 per bundle; ventral chaetae all equally thin, with upper tooth 1.5 times thinner and longer than lower; II with 1−4 per bundle, III−V with 3−5, posteriorly with 4−7; L = 2.5 mm ..... *Nais similis* Semernoy, 1984
[Lake Baikal]

7(5) Needle chaetae thin, acute; hair chaetae 3−3.5 times longer than needle chaetae, smooth; both hair and needle chaetae 1−3 per bundle; ventral chaetae 2−5, all with upper tooth thinner and up to 1.5 times longer than lower; L = 1.5−6 mm, n = 11−18 (Fig. 12.8(31−34)) ..... *Nais pseudobtusa* Piguet, 1906
[Holarctic. Afrotropical, Australia, Neotropical]

7′ Needle chaetae with apex blunt; dorsal bundles with 1−2 smooth hair chaetae and 1−2 obtuse needle chaetae, with nodulus ∼1/3 from apex; II−V ventral chaetae 2−6, distal end of lower tooth diverging from upper (and from chaeta longitudinal axis) ∼90°; teeth equally thick but upper 1.6−2 times as long as lower; VI and following with ventral chaetae 2−5, thicker and more curved, with teeth equally long or upper slightly longer but always 2−3 times thinner; L = 4−9 mm, n = 14−22 (Fig. 12.9(1−3)) ..... *Nais simplex* Piguet, 1906
[cosmopolitan]

8(4) Needle chaetae teeth long, almost parallel 9

8′ Needle chaetae teeth short, diverging 10

9(8) Dorsal bundles consisting of 1−4 hair chaetae and 1−4 needle chaetae, the latter with fine but long parallel teeth; all ventral chaetae similar, 2−5 per bundle, upper tooth twice as long and strongly curved distally, lower tooth forming right angle with chaeta longitudinal axis; L = 2.2−12 mm, n = 12−21 (Fig. 12.9(32−35)) ..... *Nais elinguis* Müller, 1774
[cosmopolitan]

9′ II−V ventral chaetae 2−5, upper tooth 1.5−2 times longer than lower; VI and following ventral chaetae usually ordinary, 2−5 per bundle, thicker and more curved, teeth subequal or upper tooth slightly longer and thinner; VI often (and in some subsequent segments) single giant chaetae per bundle, thicker, upper tooth 2−3 times as long as lower; hair chaetae 1−2, shorter than body diameter; needle chaetae 1−2, with short but distinct teeth; VIII transition of esophagus to wide midgut ("stomach"), long cells projecting as brown appendages into cavity; L = 2.5−9 mm, n = 13−21 (Fig. 12.9(17−22)) ..... *Nais pardalis* Piguet, 1906
[Holarctic. Neotropic. Oriental]

10(8) Needle chaetae teeth distinctly visible even without immersion 11

10′ Needle chaetae teeth very fine, visible at high magnification with immersion 12

11(10) Needle chaetae teeth subequal, short; dorsal hair and needle chaetae 1−2 per bundle; ventral chaetae 2−7, in II−V longer, with upper tooth longer and thinner; VI and following shorter, often thicker and more curved, teeth subequal or upper tooth slightly longer but always thinner; esophagus abruptly dilating into midgut; able to swim; L = 4−10 mm, n = 12−21 (Fig. 12.9(36−39)) ..... *Nais variabilis* Piguet, 1906
[nearly cosmopolitan]

11′ Needle chaetae teeth larger, distinctly diverging, upper tooth slightly longer and thinner; dorsal hair and needle chaetae 1−2 per bundle; II−V ventral chaetae 2−7, with upper tooth longer and thinner; VI and following 2−6, slightly thicker and more curved, with gradually evening tooth length; mature individuals penial chaetae 2−3, either simply hooked or with upper tooth reduced; esophagus gradually dilating into midgut; not swimming; L = 1.5−12 mm, n = 10−32 (Fig. 12.9(28−31)) ..... *Nais communis* Piguet, 1906
[cosmopolitan]

12(10) Ventral chaetae upper tooth 2−2.5 times as long as lower 13

12′ Ventral chaetae upper tooth 1.2−1.5 times as long as lower; needle chaetae beyond nodulus sigmoid; dorsal hair chaetae two per bundle, needle chaetae two (seldom 3−4); II−V ventral chaetae 5−6 (rarely to eight) per bundle, longer and straighter, upper tooth 1.5−2 times as long as lower; VI and following 4−5, shorter and thicker, tooth length decreasing to 1.2−1.5; posteriormost chaetae may have subequal teeth; L = 1.9−5.1 mm, n = 15−30 ..... *Nais bekmanae* Sokolskaja, 1962
[Lake Baikal and Angara River in Siberia]

13(12) Needle chaetae above nodulus < one fourth chaetal length; hair chaetae one (seldom two), needle chaetae 2−3 per bundle; II ventral chaetae 6−8 per bundle, III−V with 5−6; from VI on 4−5, thicker, and with teeth gradually becoming equal; L = 1.8−5.3 mm ..... *Nais sokolskajae* Semernoy, 2004
[Lake Baikal]

13′ Needle chaetae above nodulus < one third chaetal length; hair chaetae two (seldom one), needle chaetae 2−4 per bundle; II ventral chaetae relatively large, 5−6 per bundle, III−V with 5−6; from VI on 4−5, slightly thinner and shorter; L = 1.3−3.2 mm; littoral (Fig. 12.10(34−36)) ..... *Nais pleomorpha* Semernoy, 2004
[Lake Baikal]

14(2) Ventral chaetae upper tooth < two times as long as lower; II−V ventral chaetae 2−6 per bundle, those of II longest; posterior segments ventral chaetae 4−7; dorsal bundles of 2−3 smooth hair chaetae and 2−4 needle chaetae; L = 2.5−3.5 mm ..... *Nais tatijanae* Semernoy, 1984
[Lake Baikal]

14′ Ventral chaetae upper tooth 2−2.5 times as long as lower, II−V with 2−3 per bundle, posterior segments with three; dorsal bundles with 1−2 smooth hair chaetae and usually two needle chaetae; L = 1.5 mm; at 700 m depth (Fig. 12.10(30−33)) ..... *Nais abissalis* Semernoy, 1984
[Lake Baikal]

Oligochaeta: Tubificida: Tubificidae: Genera (excluding Lake Baikal)

A separate key to the Tubificidae of Lake Baikal is given on p. 433.

1 Hair chaetae present 2

1′ Hair chaetae absent 65

2(1) Body surface armored: either with dark secretory papillae, with transverse rows of large epidermic glands or sensory papillae, or with fine transverse furrows incrusted with sticky secretion and foreign particles; armor often lacking on prostomium and on I−II, which can be retracted; armor can be shed, giving for a short time smoother and more transparent appearance; in most species no penial sheaths ... 3

2′ Body surface smooth, more or less transparent; penial sheaths present or lacking 17

3(2) No modified genital chaetae (bifid crotchets present or lacking at genital pores) 4

3′ Modified genital chaetae of "spermathecal type" (with grooved, spatulate or hollow distal portion) either in X, or X and XI (but can be lacking in some single individuals) 15

4(3) 1−4 transverse rows of prominent papillae or glands per segment 5

4′ Body armor either with numerous small papillae or with adhering foreign particles 8

5(4) No ventral chaetae at male pores in XI; no penial sheaths 6

5′ Three dense rows of large epidermic glands per segment; no cuticular papillae; anterior dorsal bundles of 1−6 finely pilose hair chaetae and 1−5 pectinate chaetae with 2−6 intermediate denticles as long as the main teeth; anterioventral chaetae 1−6 per bundle, with upper tooth considerably longer; posterior bundles not more than four, difference between teeth decreases posteriorly; ordinary bifid chaetae at male pores in XI; short cuticular penial sheaths present, with inverted ental collar ..... ***Troglodrilus*** **[p. 410]**

6(5) Less than three rows of prominent papillae per segment 7

6′ Papillae in 3−4 rings per segment, sometimes lacking; anterior dorsal bundles with 0−2 hair and 2−3 pectinate chaetae, the latter with 4−5 distinct intermediate denticles as long as the teeth; posteriorly 1−2 hair and two pectinate chaetae, denticles by 2−3, disappearing in terminal segments; ventral chaetae 3−5 in II−III and simple-pointed; three in IV−VI, simple-pointed, enlarged and mostly hook-shaped; 3−5 chaetae beginning from VII, bifid with upper tooth almost as long as lower in anterior segments but becoming half as long posteriorly; ventral chaetae lacking at male pores in XI; no penial sheath; L = 4.5−5 mm; groundwater ..... ***Tubifex*** [in part; **p. 412**]

7(6) Segments with 1−2 circles of prominent, light-sensory papillae, with numerous small, dark secretory papillae; anteriodorsal bundles with 3−15 thick hair chaetae and 2−4 thin pectinates, with numerous fine intermediate denticles; postclitellar dorsal chaetae sparser, tail region chaetae may be lacking; anterioventral bundles with (one) 2−4 crotchets with longer upper tooth; postclitellum ventral bundles one (two) thick, strongly sigmoid crotchet with large curved lower and tiny upper tooth; L = 15−35 mm (Fig. 12.11(6−9)) ..... *Quistadrilus multisetosus* (Smith, 1900)
[invasive: Europe. Nearctic]

7′ Each segment with one circle of papillae; postclitellar segment cross body walls with wrinkles; anteriodorsal bundles with 1−2 hair chaetae and (2)3(4) sigmoid pectinates with equal teeth and 3−5 short intermediate denticles; posteriorly only one hair and two bifid chaetae per bundle; anterior segments ventral bundles with 3−4 and posterior segments with 2−3 chaetae; anterior segment chaetae upper tooth longer than lower, in posterior chaetae teeth equal; L = 12−20 mm; groundwater ..... "*Peloscolex*" *latens* Dumnicka, 1983, species incertae sedis
[Crete: Greece]

8(4) Body wall armored with secretory papillae 9

8′ Body armored with a layer of adhering particles, sometimes in transverse wrinkles (scarce small papillae can occur caudally) 13

9(8) No organic rods in atria 10

9′ A transparent, organic rod in each atrium ..... ***Baikalodrilus*** [in part; **p. 413**]

10(9) All ventral chaetae bifid 11

10′ Chaetae in ventral bundles of II−III bifid and single simple-pointed chaetae, the latter thinner than the rest, with obtuse tip; forebody ventral bundles four, posterior with two bifid chaetae, the upper tooth slightly longer in anterior bundles but considerably shorter and thinner in mid- and hindbody, teeth not strongly curved; dorsal bundles with 4−5 thick, pilose hair chaetae and 2−4 shorter than papillae, needle-shaped pectinate chaetae, with 0−3 very fine intermediate denticles; body armored with high brownish-red papillae, except clitellum and 4−5 last segments; light sensory papillae in two transverse rows per segment; L = 15−20 mm ..... ***Embolocephalus*** [in part; **p. 414**]
[Russia: Chuckchi Peninsula]

11(10) Small, insufficiently studied worms known only from groundwater 12

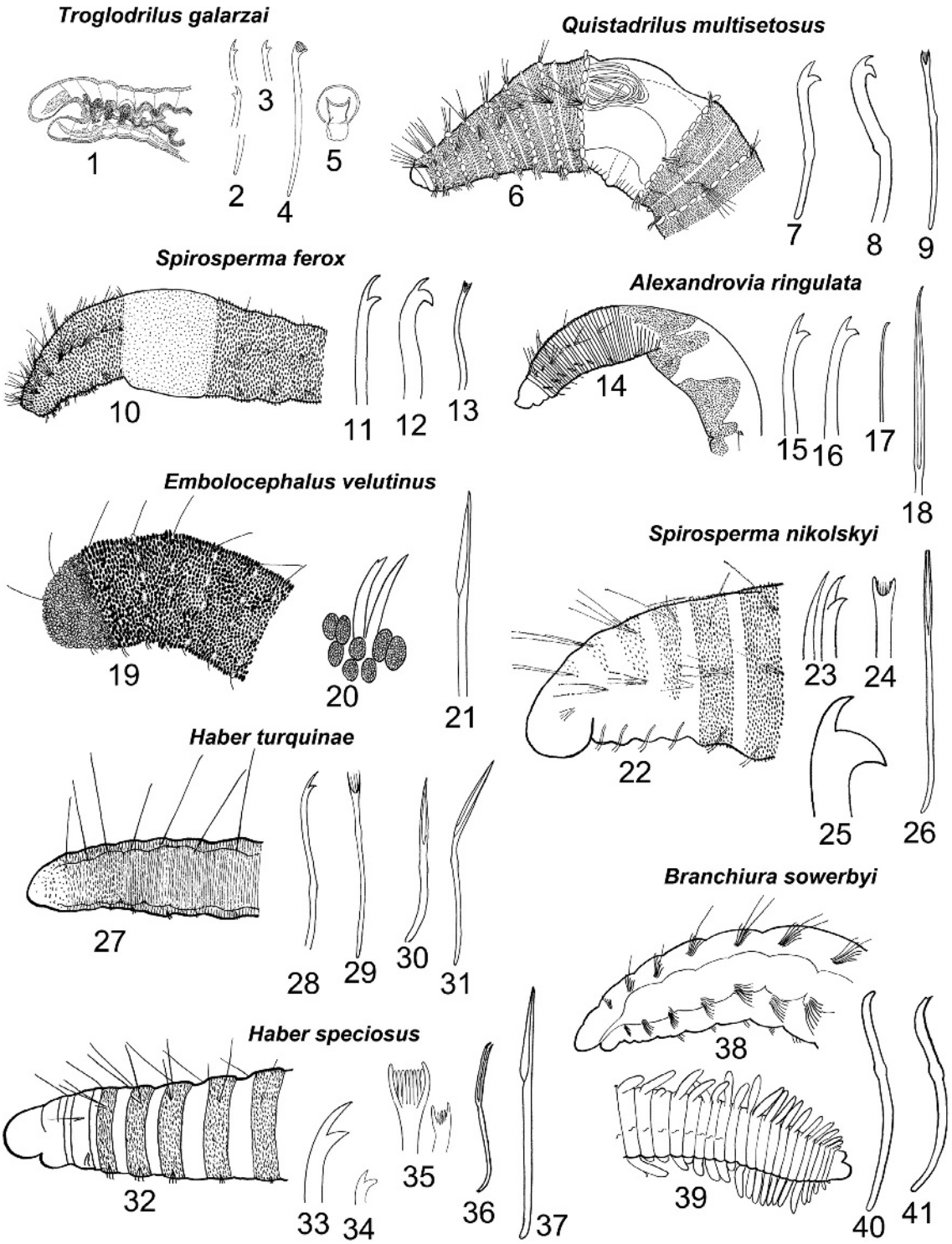


FIGURE 12.11 Tubificidae I: (1–5): *Troglodrilus galarzai*: (1) anterior end, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) pectinate chaeta, (5) penis sheath; (6–9): *Quistadrilus multisetosus*: (6) forebody of sexually mature specimen, armor lacking in clitellar region, (7) anterior ventral chaeta, (8) posterior ventral chaeta, (9) pectinate chaeta; (10–13): *Spirosperma ferox*: (10) forebody of sexually mature specimen with clitellum, (11) anterior ventral chaeta, (12) posterior ventral chaeta, (13) pectinate chaeta; (14–18): *Alexandrovia ringulata*: (14) forebody of sexually mature specimen with shedding armor, (15) anterior ventral chaeta, (16) posterior ventral chaeta, (17) needle chaeta, (18) spermathecal chaeta; (19–21): *Embolocephalus velutinus*: (19) anterior end, (20) anterior ventral bundle surrounded by armor papillae, (21) spermathecal chaeta; (22–26): *Spirosperma nikolskyi*: (22) anterior end, (23) anterior ventral bundle, (24) pectinate chaeta, (25) posterior ventral chaeta, (26) spermathecal chaeta; (27–31): *Haber turquinae*: (27) anterior end, (28) ventral chaeta, (29) pectinate chaeta, (30) genital chaeta from X, (31) genital chaeta from XI; (32–37): *Haber speciosus*; (32) anterior end, (33) anterior ventral chaeta, (34) posterior ventral chaeta, (35) pectinate chaetae, (6) genital chaeta from IX, (37) genital chaeta from XI; (38–41): *Branchiura sowerbyi*: (38) anterior end, (39) posterior end with gills, (40, 41) sigmoid chaetae.

11′ Worms of medium size, living in surface water; body covered with dense layer of irregularly arranged, dark papillae ..... ***Spirosperma*** [in part; **p. 415**]

12(11) Body armored with fine papillae arranged in transverse rows and bearing yellow secretion particles, very dense in midbody but less dense in intersegmental furrows of fore- and hindbody; above armor body is surrounded by incomplete sheath of slime and adhering sand grains; dorsal bundles consisting of one fine and short hair chaeta and one bifid chaeta with slightly longer upper tooth; ventral chaetae two, in forebody longer and with slightly longer upper tooth, posterior more curved and with teeth of equal length; mature individuals unknown; L = 2 mm; groundwater ..... "*Peloscolex*" *arganoi* Pop, 1974, incertae sedis [Turkey]

12′ Body wall transparent, armored with fine, irregularly distributed cuticular papillae and secretion drops, mostly sparse but dense on both body ends; anteriorly with a loose, incomplete sheath of sand grains cemented with slime; forebody dorsal bundles consisting of (one) 2−3 finely pilose hair chaetae and (one) 2−3 pectinate chaetae with several fine intermediate denticles as long as the main teeth; forebody ventral chaetae 2−4, in midbody two, in hindbody single; forebody upper tooth longer but not posterior; mature individuals unknown; L = 2−3 mm; groundwater ..... "*Peloscolex*" *cottarellii* Pop, 1974, incertae sedis [Turkey]

13(8) Posterior ventral chaetae not enlarged 14

13′ Posterior ventral chaetae strongly curved, thicker than the anterior ones ..... ***Spirosperma*** [in part; **p. 415**]

14(13) Body from VIII−XII covered with transverse wrinkles, with a secretion layer, distal half with adhering foreign particles; dorsal bundles 1−2 hair chaetae and 1−3 pectinate chaetae with 1−3 intermediate denticles as long as the teeth; tail region single bifid chaeta per bundle, with slightly smaller upper tooth; ventral bundles 1−4 bifid chaetae, with variable rate of teeth length; no modified genital chaetae; no penial sheath; L = 7−9 mm; brackish water, at depths of 50−200 m ..... "*Peloscolex*" *debilis* Finogenova, 1972, incertae sedis [Caspian Sea]

14′ Body plicate, covered with reddish-brown secretion; anteriodorsal bundles with 1−3 long, smooth hair chaetae and 2−3 pectinates with long parallel teeth and several shorter intermediate denticles; anterioventral bundles 2−3 simple-pointed chaetae together with 1−2 bifid ones, the latter with slightly shorter upper tooth; no ventral chaetae at male pores in XI; spermathecal pores in IX after the ordinary ventral chaetae, clitellum covering X−XI; large coelomocytes noticed in original description but not seen later; L = 8−12 mm ..... *"Rhyacodrilus"lepnevae* Malevič, 1949, incertae sedis [Russia: Lake Teleckoe]

15(3) X (or IX) modified spermathecal chaetae, with distal portion grooved, hollow or cupped; XI ventral chaetae bifid or lacking 16

15′ X and XI modified genital chaetae of "spermathecal" type ..... ***Haber*** [in part; **p. 416**]

16(15) Atria with numerous small prostate glands; body armored with dark granular secretion and foreign particles; forebody appears transversely striped due to numerous small furrows; two rows of translucent sensory papillae per segment; dorsal bundles with 1−10 very finely pilose hair chaetae and 1−6 thin needle chaetae with two very fine teeth; ventral chaetae 1−5 and with upper tooth twice as long as in anterior segments, and with equal teeth in posterior segments; X spermathecal chaetae thin, with grooved distal portion, equipped with an accessory gland; L = 4−18.5 mm (Fig. 12.11(14−18)) ..... *Alexandrovia ringulata* (Sokolskaja, 1961) [Holarctic]

16′ Atria with single large prostate gland; simple-pointed chaetae present together with bifids or without them, in some ventral bundles ..... ***Embolocephalus*** [in part; **p. 414**]

17(2) No external gills 18

17′ Tail region with digitiform gills of variable length, one dorsal and one ventral per segment; dorsal hair chaetae 1−8, short; dorsal and ventral bundles bifid chaetae with short or completely reduced upper tooth, 4−16; no modified genital chaetae; XI male pore unpaired; L = 20−270 mm (Fig. 12.11(38−41)) ..... *Branchiura sowerbyi* Beddard, 1892 [Asia. Widely introduced]

18(17) Modified genital chaetae present in sexually mature individuals 19

18′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals 42

19(18) Typical "spermathecal" chaetae (apically acute and with grooved, cupped or hollow distal portion, apparently functioning as syringe) present at spermathecal pores, in some species also (or only) at male pores 20

19′ No grooved or hollow "spermathecal" chaetae (but modified chaetae of different form may be present at genital pores) 29

20(19) Genital chaetae of "spermathecal" type (grooved) present both at spermathecal and male pores 21

20′ Genital chaetae of "spermathecal" type (grooved) either at spermathecal or at male pores only 23

21(20) Genital chaetae of spermathecal type with narrow, grooved distal portion; no forward shift of reproductive system 22

21′ Genital chaetae of spermathecal type with highly asymmetrical, mucronate or falciform distal portion, present in up to three segments, usually in all or some of VII−IX; reproductive system shifted forward after (prevailing) vegetative reproduction by architomy, male pores in IX and two pairs of spermathecal pores in VII and VIII ..... ***Potamothrix*** [in part; **p. 419**]

22(21) Genital chaetae at male pores in XI only of spermathecal type. Sperm in spermathecae arranged in spermatozeugmata ..... ***Haber*** [in part; **p. 416**]

22′ Genital chaetae at male pores in XI of two kinds, sharp "spermathecal" type and blunt type; sperm in spermathecae in bundles or amorphous ..... ***Krenedrilus*** [in part; **p. 417**]

23(20) Genital chaetae of "spermathecal" type at male pores only 24

23′ Modified spermathecal chaetae at spermathecal pores only 25

24(23) Male pores in VII with genital chaetae of "spermathecal" type; genital system shifted forward in connection with prevailing vegetative reproduction by architomy; ventral chaetae with shorter upper tooth, midbody dorsal pectinates distally widened; posterior end unsegmented and devoid of chaetae, acting as respiratory organ ..... ***Aulodrilus*** [in part; **p. 417**]

24′ Male pores in XI with genital chaetae of "spermathecal" type; ventral chaetae of X unmodified; ventral bundles with large glands, may consist of both bifid and simple chaetae ..... ***Rhyacodriloides*** **[p. 418]**

25(23) No penis sheaths 26

25′ Penis sheaths present, simultaneously with spermathecal chaetae 27

26(25) Spermathecal chaetae much thinner than ventral chaetae, bacilliform, the grooved or hollow distal portion (and terminal opening) with parallel edges while the proximal end may be slightly hooked; ventral and dorsal bifid crotchets considerably thicker and more curved in posterior segments, with large lower and small upper tooth diverging at an obtuse angle; XI male pores without ventral chaetae ..... ***Psammoryctides*** [in part; **p. 418**]

26′ Spermathecal chaetae at least as thick as ventral chaetae, often with more or less convex sides distally, if thin and with parallel edges, then usually apex solid; posterior bifid crotchets not thickened; XI male pores usually with several ordinary bifid chaetae ..... ***Potamothrix*** [in part; **p. 419**]

27(25) Penis sheaths not narrowing medially; ordinary ventral bifids in XI 28

27′ Penis sheaths short, tubular, narrow medially and slightly wider proximally; distal end widest, the margins transitioning into the penis sac inner fold; dorsal hair chaetae anteriorly 1−2 per bundle, in midbody single, in hindbody none; anteriorly 4−7, posteriorly 2−5 pectinates; anterior bundle chaetae with equal main teeth and three intermediate denticles, with longer upper tooth and two intermediate denticles; ventral bifids anteriorly 4−8 per bundle and with upper tooth twice as long as lower; posteriorly 2−5, the difference in teeth length decreasing; X with modified spermathecal chaetae, thin and with grooved distally; no ventral chaetae in XI(?); L = 13−14.5 mm; caves (Fig. 12.12(47−51)) ..... "*Psammoryctes*" *hadzii* Karaman, 1974, incertae sedis [Slovenia]

28(27) Penis sheaths thin, slightly conical, not covering the penis distal end; proximal ends fungiform, gradually transitioning into the penis sac inner fold; hair chaetae 1−3 per bundle in anterior and 1−2 posteriorly, becoming gradually shorter; pectinates 2−4 in anterior dorsal bundles, with sharp main teeth and 1−2 shorter intermediate teeth; posterior dorsal chaetae 2−3, bifid with thinner and shorter upper tooth; ventral chaetae 4−6 in anterior bundles, with subequal teeth, and reduced to two in tail region, the upper teeth becoming thinner and shorter; bifid chaetae 1−2 also ventrally in XI; modified spermathecal chaetae in X one, acute, grooved and proximal part strongly curved; bifid chaetae 1−2 ventrally in XI distal part; L = 8−10 mm ..... ***Isochaetides*** [in part; **p. 422**] [Spain]

28′ Penis sheaths thin, short cylindrical; anteriormost dorsal bundles only bifid chaetae with upper tooth twice as long and thicker than lower, 3−8 per bundle; preclitellar dorsal bundles (from IV−VIII to IX−X) 3−5 smooth hair chaetae and 5−8 bifids with equal teeth or the upper one slightly longer; dorsal bundles of genital segments only bifids; posteriorly 2−5 hair and 3−6 bifid chaetae, sometimes also simple chaetae; no pectinates; ventral bifid chaetae of similar shape, in anterior bundles 6−8, posteriorly 3−5, in IX lacking; spermathecal chaetae in X or IX single, curved, the distal part acute and grooved, the proximal part embedded in a glandular sac; 1−2 smaller bifids at male pores in X or X; L = 11−30 mm ..... ***Varichaetadrilus*** [in part; **p. 423**] [China: Lake Fuxian]

29(19) Modified genital chaetae present at male pores only (of one or two types, sometimes hidden in body wall) 30

29′ Single modified, bifid (but not grooved) spermathecal chaetae with long upper tooth present in X, blunt penial chaetae at male pores in XI; large coelomocytes abundant in body cavity ..... ***Rhyacodrilus*** [in part; **p. 423**]

30(29) Only one type of modified penial chaetae at male pores 31

30′ Two types of genital chaetae in XI ..... ***Krenedrilus*** [in part; **p. 417**]

31(30) Large coelomocytes present in body cavity 32

31′ No large coelomocytes ..... ***Tubifex*** [in part; **p. 412**]

32(31) Hair chaetae straight, not twisted 33

32′ Anterior dorsal bundle hair chaetae 1−2, thin (often broken), with distal ends twisted ..... ***Monopylephorus*** [in part; **p. 427**]

33(32) Penial chaetae more than two per bundle 34

33′ Penial chaetae 1−2 per bundle; anterior ventral upper tooth much longer than lower ..... ***Rhyacodrilus*** [in part; **p. 423**]

34(33) Penial chaetae with blunt tip or with reduced upper tooth 35

34′ XI Penial chaetae 2−3 per bundle, thin and bacilliform, gradually tapering to a sharp arched ectal end; if penial chaetae with blunt tip or with reduced upper tooth, then body wall monochrome or distal portion of bifid and pectinate chaetae dilated ..... ***Rhyacodrilus*** [in part; **p. 423**]

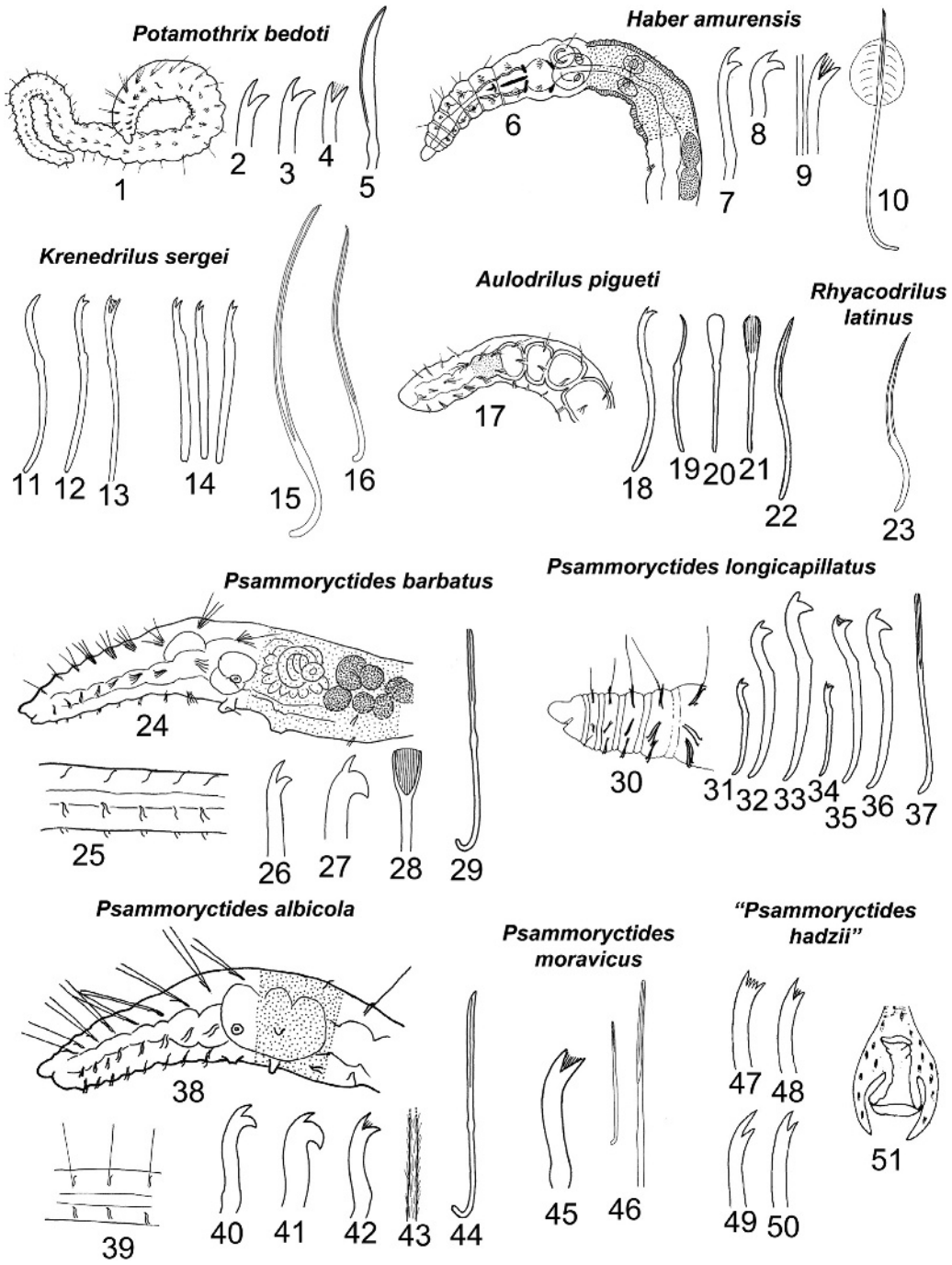


FIGURE 12.12 Tubificidae II: (1–5): *Potamothrix bedoti*: (1) general view of maturing specimen, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) pectinate chaeta, (5) genital chaeta; (6–10): *Haber amurensis:* (6) forebody of sexually mature specimen with clitellum, (7) anterior ventral chaeta, (8) posterior ventral chaeta, (9) hair and pectinate chaeta, (10) genital chaeta with surrounding gland; (11–16): *Krenedrilus sergei*: (11, 12) anterior ventral chaetae, (13) pectinate chaeta, (14) bundle of penial chaetae from XI, (15) spermathecal chaeta from X, (16) genital chaeta of spermathecal type from XI; (17–22): *Aulodrilus pigueti*: (17) anterior end of immature specimen, (18) bifid chaeta, (19–21): oar-shaped chaetae, (22) genital chaeta from VII; (23) *Rhyacodriloides latinus*, genital chaeta of spermathecal type from XI; (24–29): *Psammoryctides barbatus*: (24) forebody of sexually mature specimen with clitellum, (25) fragment of hind body, (26) anterior ventral chaeta, (27) posterior ventral chaeta, (28) pectinate (spade-like) chaeta, (29) spermathecal chaeta; (30–37): *Psammoryctides longicapillatus:* (30) anterior end, (31) anterior ventral chaeta, (32) ventral chaeta from midbody, (33) posterior ventral chaeta, (34) anterior pectinate chaeta, (35) pectinate chaeta from midbody, (36) posterior dorsal chaeta, (37) spermathecal chaeta; (38–44): *Psammoryctides albicola*: (38) forebody of sexually mature specimen with clitellum, (39) fragment of hind body, (40) anterior ventral chaeta, (41) posterior ventral chaeta, (42) pectinate chaeta, (43) fragment of hair chaeta, (44) spermathecal chaeta; (45, 46) *Psammoryctides moravicus*: (45) pectinate chaeta, (46) spermathecal chaeta (at two magnitudes); (47–51): "*Psammoryctides*" *hadzii*: (47) anterior pectinate chaeta, (48) posterior pectinate chaeta, (49) anterior ventral chaeta, (50) posterior ventral chaeta, (51) penis sheath in penial sac.

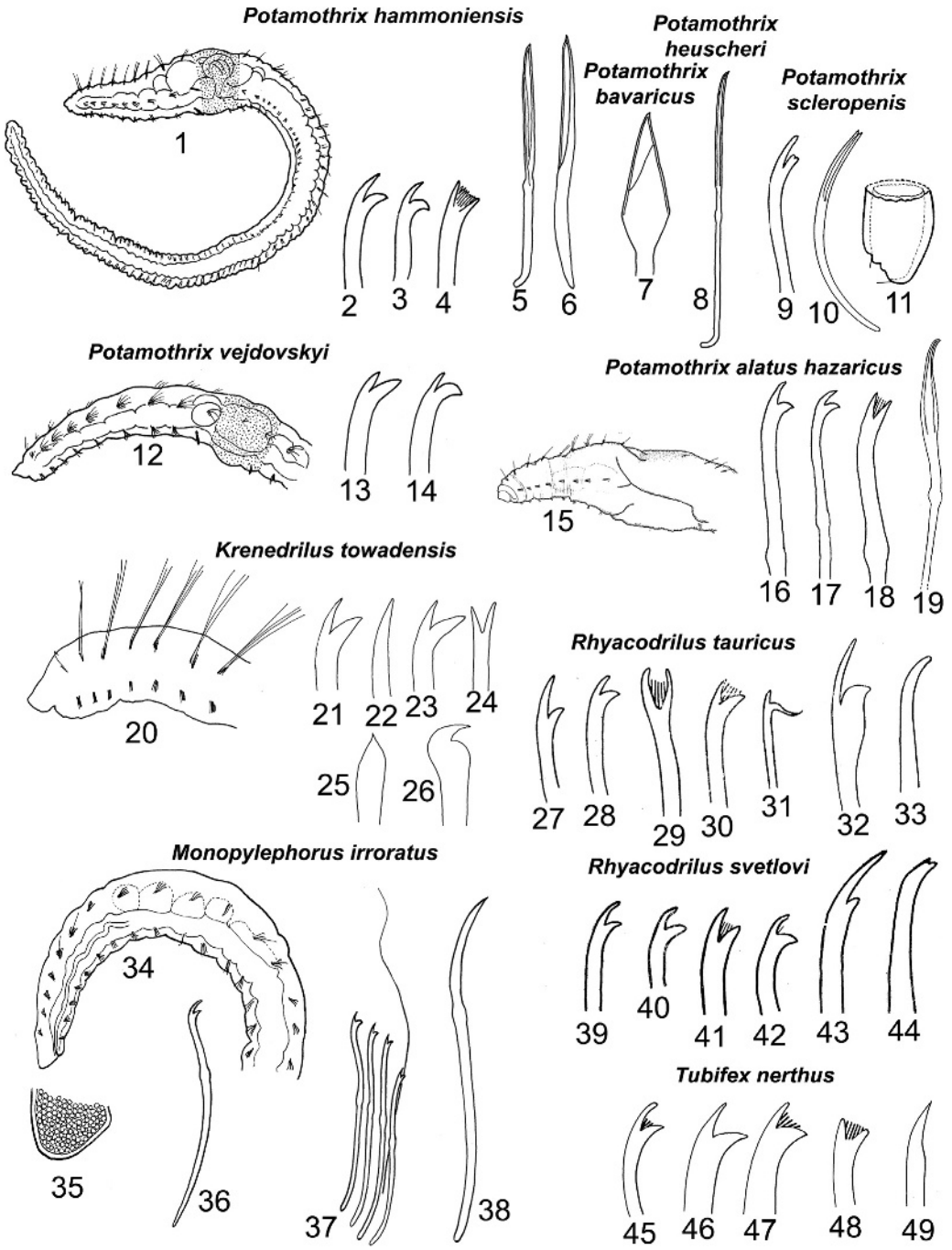


FIGURE 12.13 Tubificidae III: (1–6): *Potamothrix hammoniensis:* (1) general view of sexual mature specimen with clitellum, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) pectinate chaeta, (5, 6) spermathecal chaetae; (7) *Potamothrix bavaricus*, spermathecal chaeta: (8) *Potamothrix heuscheri*, spermathecal chaeta; (9–11): *Potamothrix scleropenis*: (9) ventral chaeta, (10) spermathecal chaeta, (11) penis sheath; (12–14): *Potamothrix vejdovskyi*: (12) forebody of sexual mature specimen with clitellum, (13) anterior bifid chaeta, (14) posterior bifid chaeta; (15–19): *Potamothrix alatus hazaricus*: (15) forebody of sexual mature specimen with clitellum, (16) anterior ventral chaeta, (17) posterior ventral chaeta, (18) pectinate chaeta, (19) spermathecal chaeta; (20–26): *Krenedrilus towadensis*: (20) anterior end, (21, 22) anterior ventral chaetae, (23) posterior ventral chaeta, (24) dorsal bifid chaeta, (25, 26) two different kinds of penial chaetae; (27–33): *Rhyacodrilus tauricus*: (27) anterior ventral chaeta, (28) posterior ventral chaeta, (29) anterior pectinate chaeta, (30) pectinate chaeta from midbody, (31) posterior dorsal chaeta, (32) spermathecal chaeta, (33) penial chaeta; (34–38): *Monopylephorus irroratus*: (34) forebody, (35) prostomium filled with coelomocytes, (36) ventral chaeta, (37) dorsal bundle, (38) penial chaeta; (39–44): *Rhyacodrilus svetlovi*: (39) anterior ventral chaeta, (40) posterior ventral chaeta, (41) anterior pectinate chaeta, (42) posterior pectinate chaeta, (43) spermathecal chaeta, (44) penial chaeta; (45–49): *Tubifex nerthus*: (45) anterior ventral pectinate chaeta, (46, 47) posterior ventral chaetae, (48) dorsal pectinate chaeta, (49) penial chaeta.

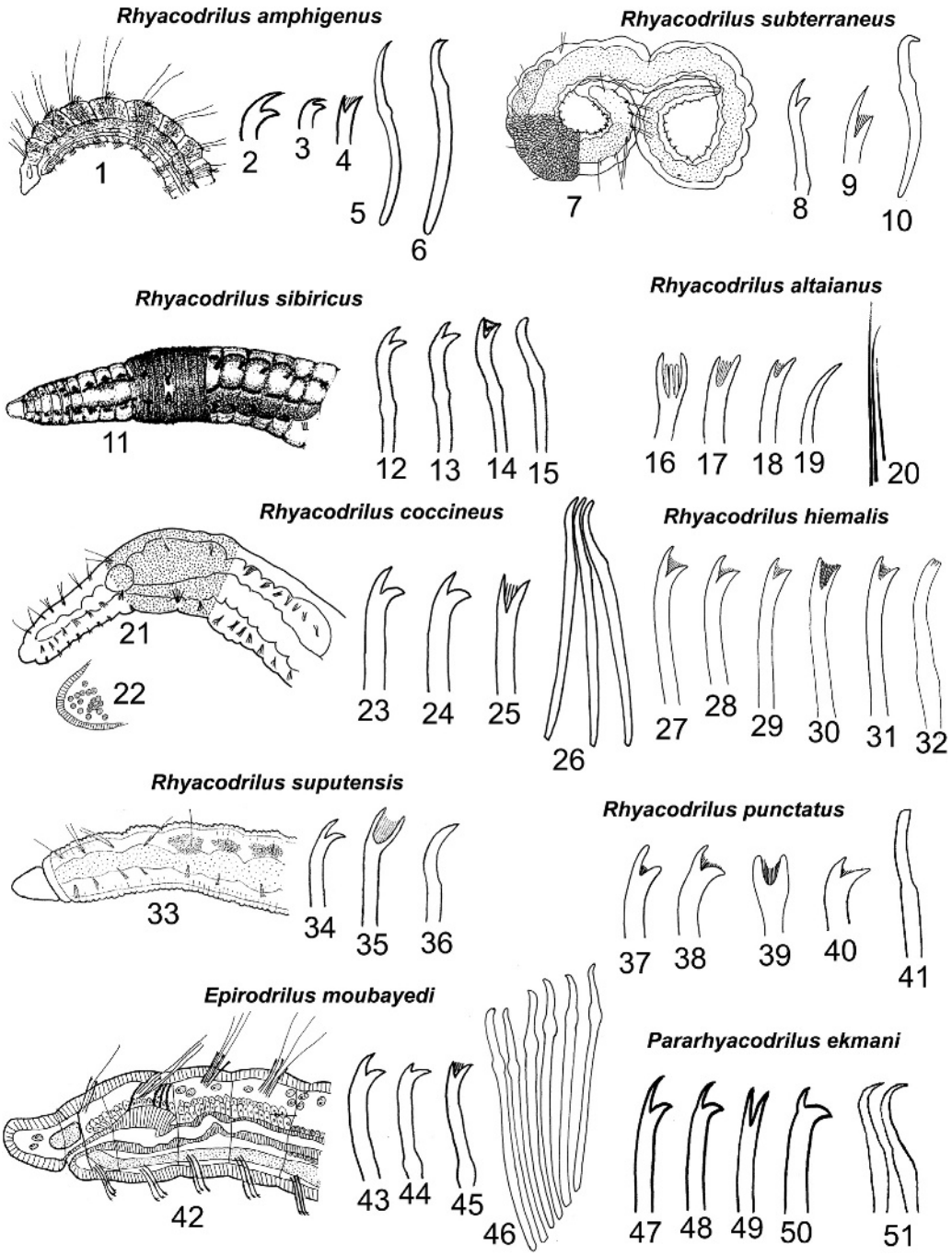


FIGURE 12.14 Tubificidae IV: (1–6): *Rhyacodrilus amphigenus*: (1) anterior end, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) anterior dorsal pectinate chaeta, (5) posterior dorsal chaeta, (6) penial chaeta; (7–10): *Rhyacodrilus subterraneus*: (7) general view of sexually mature specimen with clitellum, (8) ventral chaeta, (9) dorsal pectinate chaeta, (10) penial chaeta; (11–15): *Rhyacodrilus sibiricus*: (11) forebody of sexually mature specimen with clitellum, (12) anterior ventral chaeta, (13) posterior ventral chaeta, (14) dorsal pectinate chaeta, (15) penial chaeta; (16–20): *Rhyacodrilus altaianus:* (16) anterior dorsal chaeta, (17, 18) dorsal chaetae from midbody, (19) posterior dorsal chaeta, (20) bundle of penial chaetae; (21–26): *Rhyacodrilus coccineus*: (21) forebody of sexually mature specimen with clitellum, (22) prostomium with coelomocytes, (23) anterior ventral chaeta, (24) posterior ventral chaeta, (25) dorsal pectinate chaeta, (26) bundle of penial chaetae; (27–32): *Rhyacodrilus hiemalis*: (27) anterior ventral pectinate chaeta, (28, 29) posterior ventral pectinate chaetae, (30) anterior dorsal pectinate chaeta, (31) posterior dorsal pectinate chaeta, (32) penial chaeta; (33–36): *Rhyacodrilus suputensis:* (33) anterior end, (34) ventral chaeta, (35) dorsal pectinate chaeta, (36) penial chaeta; (37–41): *Rhyacodrilus punctatus:* (37) anterior ventral pectinate chaeta, (38) posterior ventral pectinate chaeta, (39) anterior dorsal pectinate chaeta, (40) posterior dorsal pectinate chaeta, (41) penial chaeta; (42–46): *Epirodrilus moubayedi*: (42) anterior end, (43) anterior ventral chaeta, (44) posterior ventral chaeta, (45) dorsal pectinate chaeta, (46) bundle of penial chaetae; (47–51*): Pararhyacodrilus ekmani*: (47) anterior ventral chaeta, (48) posterior ventral chaeta, (49) anterior dorsal chaeta, (50) posterior dorsal chaeta, (51) bundle of penial chaetae.

35(34) Hair chaetae present in several anterior dorsal bundles but lacking in postclitellar segments 36

35′ Hair chaetae present also in midbody 38

36(35) Pseudopenes usually not protruded 37

36′ Pseudopenes permanently protruded, if not, then X ventral chaetae teeth length difference increasing posteriorly ..... ***Rhyacodrilus*** [in part; **p. 423**]

37(36) Spermathecae connected by a short duct to intestine ..... ***Pararhyacodrilus*** [in part; **p. 428**] [Denmark]

37′ Spermathecae not connected with intestine ..... ***Rhyacodrilus*** [in part; **p. 423**] [Russia]

38(35) Ventral chaetae not pectinate, penial chaetae bifid or blunt-tipped 39

38′ Ventral chaetae all pectinate; penial chaetae with distal ends split into several short denticles ..... ***Rhyacodrilus*** [in part; **p. 423**]

39(38) Pectinate chaetae present in anterior dorsal bundles; posterior bifid chaetae upper tooth not very short and erect 40

39′ Anterior dorsal bundle bifid crotchets 4−5, with equal parallel teeth (without pectination?); posterior bundles 2−3 crotchets, the lower tooth becoming gradually thicker and more curved, but upper one thin, short and erect ..... ***Pararhyacodrilus*** [in part; **p. 428**] [Sweden]

40(39) No "anchorage bridge" between the spermathecal pores 41

40′ Anterior dorsal bundles 2−5 smooth hair chaetae and 2−5 pectinates, with slightly longer upper tooth, with short fine intermediate denticles; midbody 1−2 hair and 2−4 bifid chaetae, caudally only 1−2 bifid crotchets; anterior ventral chaetae 3−6, with slightly longer upper tooth; teeth become equal in dorsal and ventral crotchets caudally; penial chaetae ≤8 per bundle, with simple slightly bent tip; X with an unpaired, longitudinal elevation ("anchorage bridge" for attaching of penial chaetae during copulation) between spermathecal pores; L = 14 mm ..... *Peristodrilus montanus* (Hrabě, 1962) [southern Europe]

41(40) Anterior dorsal bundles with ≥ three smooth hair chaetae; L = 15−35 mm ..... ***Rhyacodrilus*** [in part; **p. 423**]

41′ Smaller worms, shorter than 10 mm; not more than three hair chaetae per bundle. Atria very long, consisting of two dilated portions ..... ***Epirodrilus*** [in part; **p. 428**]

42(18) Penis sheaths present 43

42′ No penis sheaths (sometimes cuticle of penis thickened remembering penis sheath) 53

43(42) Ordinary bifid chaetae at male pores in XI 44

43′ No ventral chaetae in XI at male pores 49

44(43) Penis sheaths at least as long as wide; ventral chaetae without intermediate denticles 45

44′ Penis sheaths thin-walled and very short, surrounding only penis distal portion; ventral bifids (pectinates) 2−3 anteriorly, upper tooth longer than lower, and a single intermediate denticle ..... ***Varichaetadrilus*** [in part; **p. 423**]

45(44) Penis sheaths of different shape; no especially thickened and curved bifid chaetae; no fragmentation 46

45′ Penis sheaths length ~twice as expanded proximal portion width; distal end wider than middle; reproducing mainly by fragmentation, seldom maturin ..... ***Varichaetadrilus*** [in part; **p. 423**]

46(45) Penis sheaths cylindrical or ovoid 47

46′ Penis sheaths ovoid, distally narrower; no spermathecae; anterior dorsal bundles 2−3 pilose hair chaetae and three pectinates with slightly longer upper tooth and small intermediate denticles; posteriorly one hair and one bifid chaeta; anterior ventral bundles 3−5 bifid chaetae, posteriorly one per bundle, with considerably longer upper tooth; XI two ordinary bifids; spermathecae; two pairs of dilated lateral vessels ("hearts"), in IX and X; L = 6 mm. Amur River, Russian Far East ..... ***Tubifex*** [in part; **p. 412**]

47(46) Hair chaetae less numerous, pectinate chaetae with rough intermediate denticles; penis sheaths without collar 48

47′ Anterior hair chaetae 4−7, postclitellar one per bundle; pectinate chaetae with diverging teeth and a film of fine intermediate denticles, 7−9 in anterior bundles and three in posterior ones; anterior ventral chaetae 7−11, with equally thick teeth, upper tooth longer; posteriorly 2−3, upper tooth longer and thinner; "hearts" in VIII; penis sheaths very small, tubular with symmetrical distal end and proximal collar; L = up to 25 mm ..... "*Tubifex*" *solitarius* (Semernoy, 1972), incertae sedis [Russia: Transbaikalia. Not *Tasserkidrius solitarius* sensu Semernoy (2004), p. 240]

48(47) Penis sheaths (?) short cylindrical, very thin, not seen in all specimens; ordinary bifid chaetae at male pores in XI(?); all dorsal bundles 1−6 very finely pilose hair chaetae and 3−7 pectinate or palmate chaetae, the latter with curved distal portion and 5−14 intermediate denticles, with length equal to main teeth; anterior ventral chaetae 4−6, with upper tooth slightly longer and thinner; posteriorly decreasing to 2−3, while teeth become subequal but the upper tooth thinner; L = 17 mm ..... ***Ilyodrilus*** [in part; **p. 428**] [Russia: Kuril Archipelago]

48′ Penis sheaths short, funicular; anterior dorsal bundles 0−3 smooth hair and (2) 3−4 (5) pectinate chaetae; the latter with equal teeth and (two) 3−5 rough intermediate denticles; postclitellar segments with hair chaetae diminishing while the pectinates are replaced by bifids, their number decreasing to 1−3 (four); anterior bundle ventral chaetae 3−6 (eight), posteriorly 2−5, upper tooth being slightly longer in anterior and shorter in the most posterior bundles; XI at male pores 2−3 ordinary bifids present (but sometimes absent); L = 6−7 mm (Fig. 12.15(12−17)) ..... ***Peipsidrilus*** [in part; **p. 429**]
[Lebanon, Turkey]

49(43) Penis sheaths truncate conical or funicular, with terminal distal opening 50

49′ Penis sheaths proximal end funicular, sharp blind tip, and lateral distal opening ..... ***Tasserkidrilus*** [in part; **p. 429**]

50(49) No fragmentation, no forward shift of genital system; ventral chaetae present in X 51

50′ No ventral chaetae at spermathecal and male pores located in X−XI or VIII−IX, respectively; reproductive system forward shift supposedly connected with architomy (fragmentation); dorsal bundles with 1−6 smooth hair chaetae and 1−4 pectinates, the latter with relatively long and straight teeth and 1−3 slightly shorter intermediate denticles; ventral bifids 1−5, with equal teeth or upper tooth slightly longer, often with tiny intermediate denticle; all three kinds of chaetae present in postclitellar segments but in smaller number; penis sheaths as delicate truncated cones; L = ∼6 mm (Fig. 12.15(29−33)) ..... ***Peipsidrilus*** [in part; **p. 429**]
[northern Europe]

51(50) Penis sheaths short truncated conical or funicular, with distal end oblique; dorsal chaetae intermediate denticles small or lacking 52

51′ Penis sheaths prolonged conical or funicular, length ∼three times proximal width; dorsal pectinates with rough intermediate denticles ..... ***Tubifex*** [in part; **p. 412**]

52(51) Penis sheaths truncate conical or longer than wide ..... ***Ilyodrilus*** [in part; **p. 428**]

52′ Penis sheaths about as long as wide, conical with funicular proximal and narrow, tubular distal portion ..... ***Tubifex*** [in part; **p. 412**]

53(42) XI male pores without ventral chaetae 54

53′ XI male pores with unmodified (usually bifid) ventral chaetae (seldom in VII or X) 56

54(53) Bifids not much thicker in the posterior segments, present in X and lacking in XI only 55

54′ Midbody and tail region scarce, thick and strongly curved bifids in all bundles, with thick lower and much shorter and thinner upper tooth. Ventral chaetae lacking in XI and XI ..... ***Psammoryctides*** [in part; **p. 418**]

55(54) No coelomocytes; ventral chaetae 1−4, with conspicuously shorter upper tooth; dorsal bundles with 1−4 smooth hair chaetae and two to four pectinates with subequal, slender teeth and 2−3 small intermediate denticles; L > 13 mm..... ***Aulodrilus*** [in part; **p. 417**]

55′ Large coelomocytes abundant. Ventral chaetae with longer upper tooth in anterior but with shorter one in posterior segments ..... ***Epirodrilus*** [in part; **p. 428**]

56(53) Pectinate chaetae in dorsal bundles only, or lacking 57

56′ Similar pectinate chaetae with 2−3 rough intermediate denticles present in all bundles, dorsal and ventral, including X and XI (may be lacking in XI); main teeth equal in dorsal pectinates but upper tooth is slightly longer in ventral ones; pectinates number 3−5 (six) in anterior dorsal and (two) 3−4 in posterior dorsal bundles, 4−6 (seven) and 3−4 in ventral bundles, respectively; hair chaetae 2−4 in fore- and midbody but only two in tail region, very finely pilose; L = 5.0−9.6 mm; groundwater ..... *Sketodrilus flabellisetosus* (Hrabě, 1966)
[Slovenia, Italy]

57(56) Bifid chaetae (but not always pectinates if present) with upper tooth shorter 58

57′ Bifid chaetae at least in most anterior bundles with equal teeth, or the upper tooth longer 62

58(57) No large coelomocytes; all crotchets bifid, not simple-pointed 59

58′ Large coelomocytes abundant; anterior dorsal bundles one hair chaeta (seldom two) and two to three bifids with shorter and thinner upper tooth; posterior dorsal bundles with 3−4 simple-pointed crotchets ..... ***Rhyacodrilus*** [in part; **p. 423**]

59(58) Hair chaetae in anterior segments one to two or lacking; no architomy; posterior end not modified as respiratory organ 60

59′ Hair chaetae numerous, short; asexual reproduction by architomy (fragmentation) prevailing, sexual maturation rare; posterior end thin and unsegmented, acting as respiratory organ ..... ***Aulodrilus*** ([in part; **p. 417**]

60(59) Hair and pectinate chaetae present in preclitellar bundles 61

60′ Dorsal hair chaetae present only in postclitellar segments, short, 1−2 per bundle; no pectinates ..... ***Potamothrix*** [in part; **p. 419**]

61(60) Ventral bifid chaetae in anterior bundles 2−3 (four), sigmoid and thick, with equally long teeth but upper tooth shorter; posterior region only 1−2 bifids both in dorsal and ventral bundles, larger than in forebody, upper tooth becoming gradually smaller and angle between teeth larger; dorsal hair chaetae 1−2 in fore- and midbody, pilose; dorsal pectinate chaetae 1−4, sigmoid, thick, with equally thick, short teeth, and 2−5 much shorter intermediate teeth..... ***Psammoryctides*** [in part; **p. 418**]

61′ Ventral chaetae thin, with slightly shorter upper tooth, anteriorly 2−6, posteriorly two; anterior dorsal bundles with 1−2 thin hair chaetae and 1−4 pectinates, the latter with equally long teeth and 1−3 intermediate denticles ..... ***Tubifex*** [in part; **p. 412**]

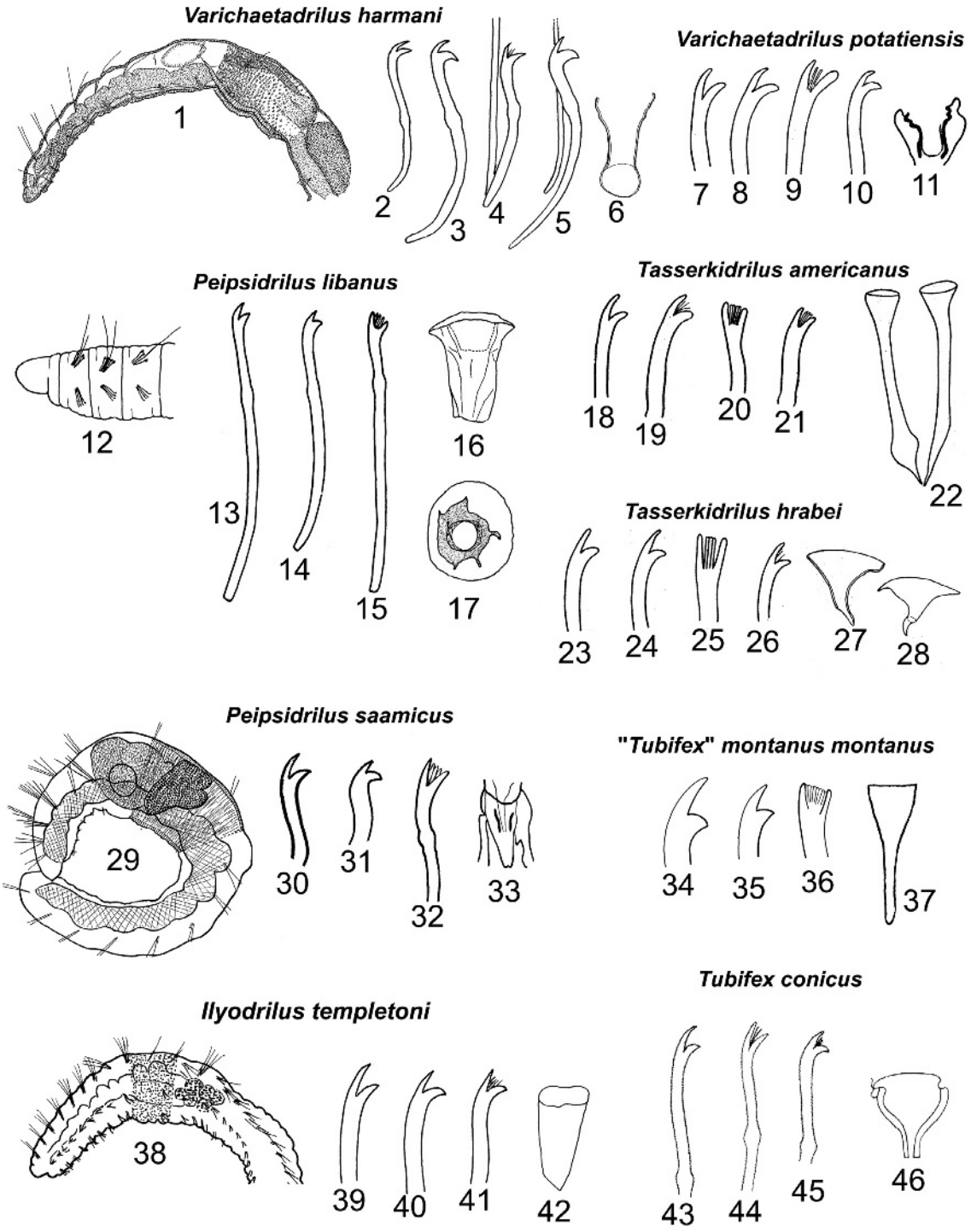


FIGURE 12.15 Tubificidae V: (1–6): *Varichaetadrilus harmani:* (1) forebody of sexually mature specimen with clitellum, (2) anterior ventral chaeta, (3) posterior ventral chaeta, (4) anterior hair and pectinate chaeta, (5) posterior hair and bifid chaeta, (6) penis sheath; (7–11): *Varichaetadrilus potatiensis*: (7) anterior ventral chaeta, (8) posterior ventral chaeta, (9) anterior pectinate chaeta, (10) posterior dorsal chaeta, (11) penis sheath with penis in penial sac; (12–17): *Peipsidrilus libanus:* (12) anterior end, (13) anterior ventral chaeta, (14) posterior ventral chaeta, (15) pectinate chaeta, (16) penis sheath in lateral view, (17) penis sheath in apical view; (18–22): *Tasserkidrilus americanus*: (18) ventral bifid chaeta, (19) ventral pectinate chaeta, (20) anterior dorsal pectinate chaeta, (21) posterior dorsal pectinate chaeta, (22) two penis sheaths in different lateral aspects; (23–28): *Tasserkidrilus hrabei*: (23) anterior ventral chaeta, (24) posterior ventral chaeta, (25) anterior pectinate chaeta, (26) posterior pectinate chaeta, (27, 28) penis sheaths in different lateral aspects; (29–33): *Peipsidrilus saamicus*: (29) general view of sexually mature specimen with clitellum, (30) anterior ventral chaeta, (31) posterior ventral chaeta, (32) pectinate chaeta, (33) penis sheath with penis in penial sac; (34–37): "*Tubifex*" *montanus montanus*: (34) anterior ventral chaeta, (35) posterior ventral chaeta, (36) pectinate chaeta, (37) penis sheath; (38–42): *Ilyodrilus templetoni*: (38) forebody of sexually mature specimen with clitellum, (39) anterior ventral chaeta, (40) posterior ventral chaeta, (41) pectinate chaeta, (42) penis sheath; (43–46): *Tubifex conicus*: (43) ventral chaeta, (44) anterior pectinate chaeta, (45) posterior pectinate chaeta, (46) penis sheath.

62(57) Body not filiform; no extremely long and flexible hair chaetae 63

62′ Tail region extremely long and thin, filiform with extended segments; forebody hair chaetae 2−5 per bundle, postclitellar segments with one, extremely long, thin and flexible; anterior dorsal bundle pectinates 2−3, bayonet-shaped, teeth equal, 1−2 intermediate denticles; forebody ventral bifids 1−4 per bundle, with upper tooth slightly longer; posterior teeth equal or upper tooth shorter; L = to 70 mm (Fig. 12.16(12−15)) ..... *Lophochaeta ignota* Štolc, 1886 [Palaearctic. Nearctic, Neotropics]

63(62) Ventral chaetae in hindbody with longer upper tooth 64

63′ Ventral chaetae in hindbody with equal teeth or the upper tooth smaller ..... ***Tubifex*** [in part; **p. 412**]

64(63) Prostomium very small, mouth large, pharynx folded and eversible; dorsal hair chaetae begining in IV, short and bayonet-shaped, smooth or pilose, 2−5 per bundle; bifid crotchets anteriorly (one) 2−6 dorsally and (one) 2−7 in ventral bundles, with subequal teeth or upper tooth shorter in II−III, with distinctly longer upper tooth in following segments; bifids may be stouter, sometimes single, with shorter upper tooth in II, lacking in III; no pectinates; posterior segments bifids 2−3 in dorsal and 2−4 in ventral bundles; no modified genital chaetae; spermathecae often absent; L = 7−25 mm (Fig. 12.16(22−25)) ..... *Teneridrilus mastix* (Brinkhurst, 1978) [eastern Palaearctic. Nearctic]

64′ Mouth and pharynx not enlarged; chaetae in II not enlarged, not lacking in III; dorsal hair chaetae 1−2 per bundle, present along whole body; fore- and midbody 3−5 pectinate chaetae with equal teeth and 3−4 intermediate denticles; hindbody with 2−3 bifid chaetae with equal teeth; anteriorly ventral bifid chaetae 3−5, rearward 3−4, all with longer upper tooth like dorsal bifids ..... ***Potamothrix*** [in part; **p. 419**]

65(1) Body wall armored with papillae 66

65′ Body wall smooth 67

66(65) Body wall transparent but armored with fine, irregularly distributed cuticular papillae and variable secretion drops, more dense in hindbody; a loose sheath of sand grains cemented with slime; dorsal and ventral bundles 4−5 (six) per bundle, all with lower tooth length twice and thicker than upper; hindbody chaetae characteristically tapering distally; L = 5 mm; groundwater ..... *"Peloscolex" boitanii* Pop, 1974, incertae sedis [Turkey]

66′ Adults with thin tail region (immatures with entire body) covered with small, sparse secretory papillae, the anterior, thicker region smooth; anterior bundles with 2−5 bifid chaetae with short equal teeth; posterior segments 1−2 simple-pointed, acute chaetae; transtional zone sometimes bifids with prolonged teeth, lower tooth thinner; no modified genital chaetae, no penis sheaths; L = 7−9 mm; slightly brackish water and freshwater in river mouths (Fig. 12.17(1−4)) ..... *Tubificoides heterochaetus* (Michaelsen, 1926) [Europe. Nearctic]

67(65) All or most dorsal chaetae palmate; no penis sheaths 68

67′ No palmate chaetae; penis sheaths present or absent 69

68(67) All dorsal chaetae palmate with 5−8 intermediate denticles as long as main teeth, 6−15 in anterior bundles and 2−6 (eight) posteriorly; ventral chaetae mostly pectinate, with longer upper tooth and with 1−3 short intermediate denticles, 5−10 per bundle anteriorly and 2−5 posteriorly; XI male pores without ventral chaetae; penis sheaths absent; L = 7−20 mm ..... ***Isochaetides*** [in part; **p. 422**]

68′ Anteriormost bundles, both dorsal and ventral, with up to 10 chaetae, simple or with rudimentary upper tooth; from ∼VI−X posteriorly chaetae becoming palmate, with numerous intermediate denticles forming together with short main teeth a broad lobe, mostly eight per bundle; similar chaetae, fewer in number, in hindbody, and ventrally in XI, at male pores (Fig. 12.17(5−6)) ..... ***Aulodrilus*** [in part; **p. 417**]

69(67) At least some chaetae bifid 70

69′ All chaetae simple-pointed; XI without ventral chaetae; penis sheaths present ..... ***Limnodrilus*** [in part; **p. 430**]

70(69) Simple-pointed locomotory (not genital) chaetae present, accompanied with bifids with shorter upper tooth 71

70′ No simple-pointed locomotory chaetae (with exception of some small groundwater forms with a few simple-pointed chaetae in posterior segments) 74

71(70) No enlarged ventral chaetae; no penis sheaths 72

71′ Chaetae with shorter or rudimentary upper tooth or simple-pointed, in some anteriormost bundles 2−3 per bundle, most bundles single; ventral chaetae becoming gradually very large and hooked in VI−IX and smaller again posteriorly, lacking in XI; dorsal chaetae smaller than ventral; penis sheaths short, truncated, thin-walled cones; L = 36−38 mm (Fig. 12.20(51−55)) ..... *Lycodrilides schizochaetus* (Michaelsen, 1901) [Russia: Lake Baikal, Angara and Enisej Rivers]

72(71) Anteriormost segments with simple-pointed chaetae; XI male pores with no ventral chaetae; larger worms, not connected with groundwater 73

72′ Locomotory chaetae of three kinds: in forebody two to three with shorter upper tooth, midbody and tail region two simple-pointed, small and sharp ventrally, larger and more obtuse dorsally; XI penial bundles consisting of 4−5 parallel, sigmoid chaetae with simple thin tip; midgut widening only behind clitellum; L = 3−3.5 mm (Fig. 12.17(39−42)) ..... ***Gianius*** [in part; **p. 431**] [Turkey]

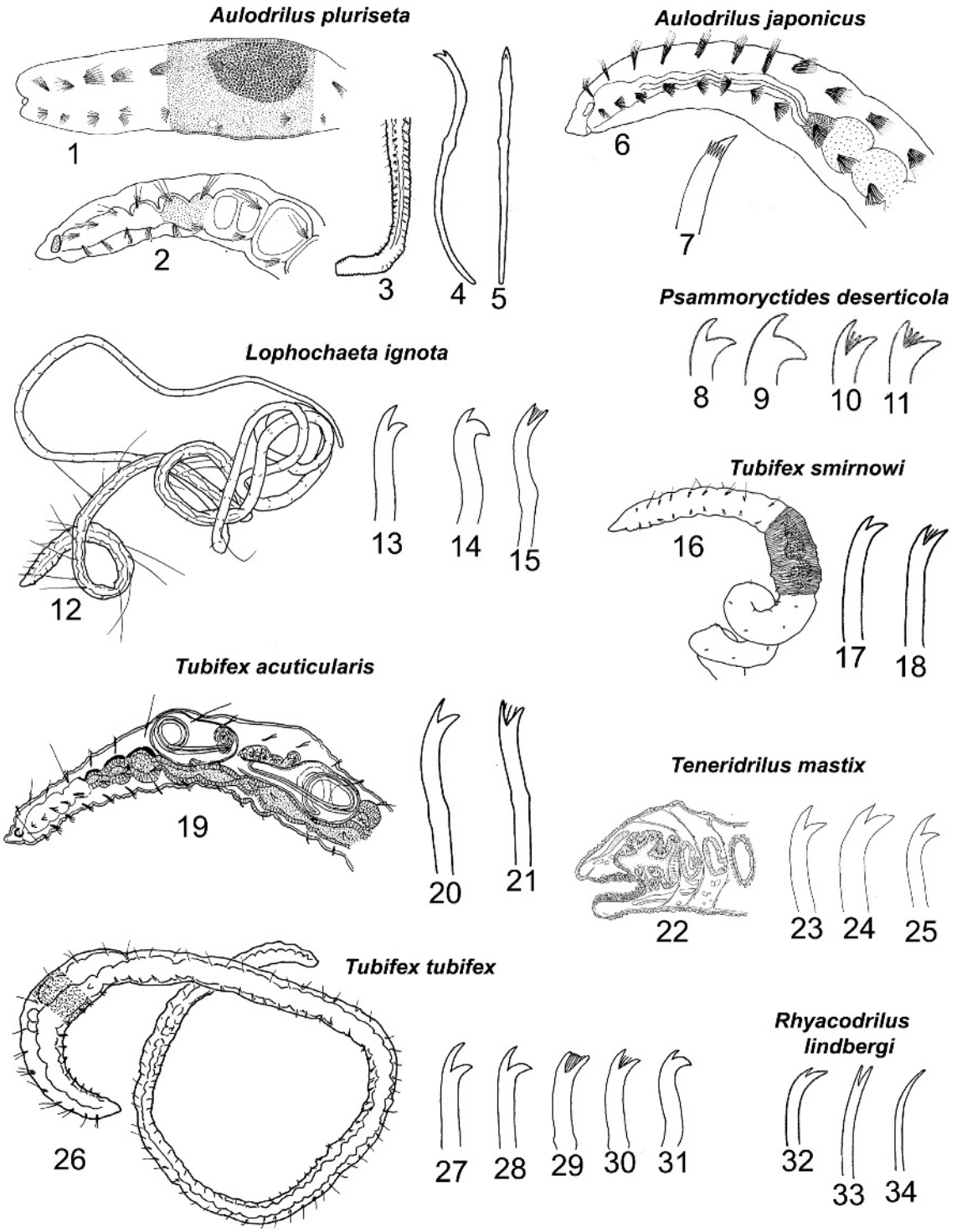


FIGURE 12.16 Tubificidae VI: (1–5): *Aulodrilus pluriseta*: (1) forebody of sexually mature specimen with clitellum, (2) forebody of immature specimen, (3) unsegmented posterior end, (4, 5) two aspects of bifid chaetae; (6, 7) *Aulodrilus japonicus*: (6) forebody of immature specimen, (7) "bifid" chaeta with split upper tooth; (8–11): *Psammoryctides deserticola:* (8) anterior ventral chaeta, (9) posterior ventral chaeta, (10) anterior dorsal chaeta, (11) posterior dorsal chaeta; (12–15): *Lophochaeta ignota*: (12) general view of sexually immature specimen, (13) anterior ventral chaeta, (14) posterior ventral chaeta, (15) anterior dorsal chaeta; (16–18): *Tubifex smirnowi*: (16) forebody of sexually mature specimen with clitellum, (17) ventral chaeta, (18) dorsal chaeta: (19–21): *Tubifex acuticularis*: (19) forebody of sexually mature specimen with clitellum, (20) ventral chaeta, (21) anterior dorsal chaeta; (22–25): *Teneridrilus mastix*: (22) sagittal section of anterior end demonstrating the folded pharynx, (23, 24) anterior bifid chaetae, (25) posterior bifid chaeta; (26–31): *Tubifex tubifex*: (26) general view of sexually mature specimen with clitellum, (27) anterior ventral chaeta, (28) ventral chaeta from midbody, (29) anterior dorsal chaeta, (30) dorsal chaeta from midbody, (31) posterior chaeta; (32–34): *Rhyacodrilus lindbergi*: (32) ventral chaeta, (33) anterior dorsal chaeta, (34) posterior dorsal chaeta.

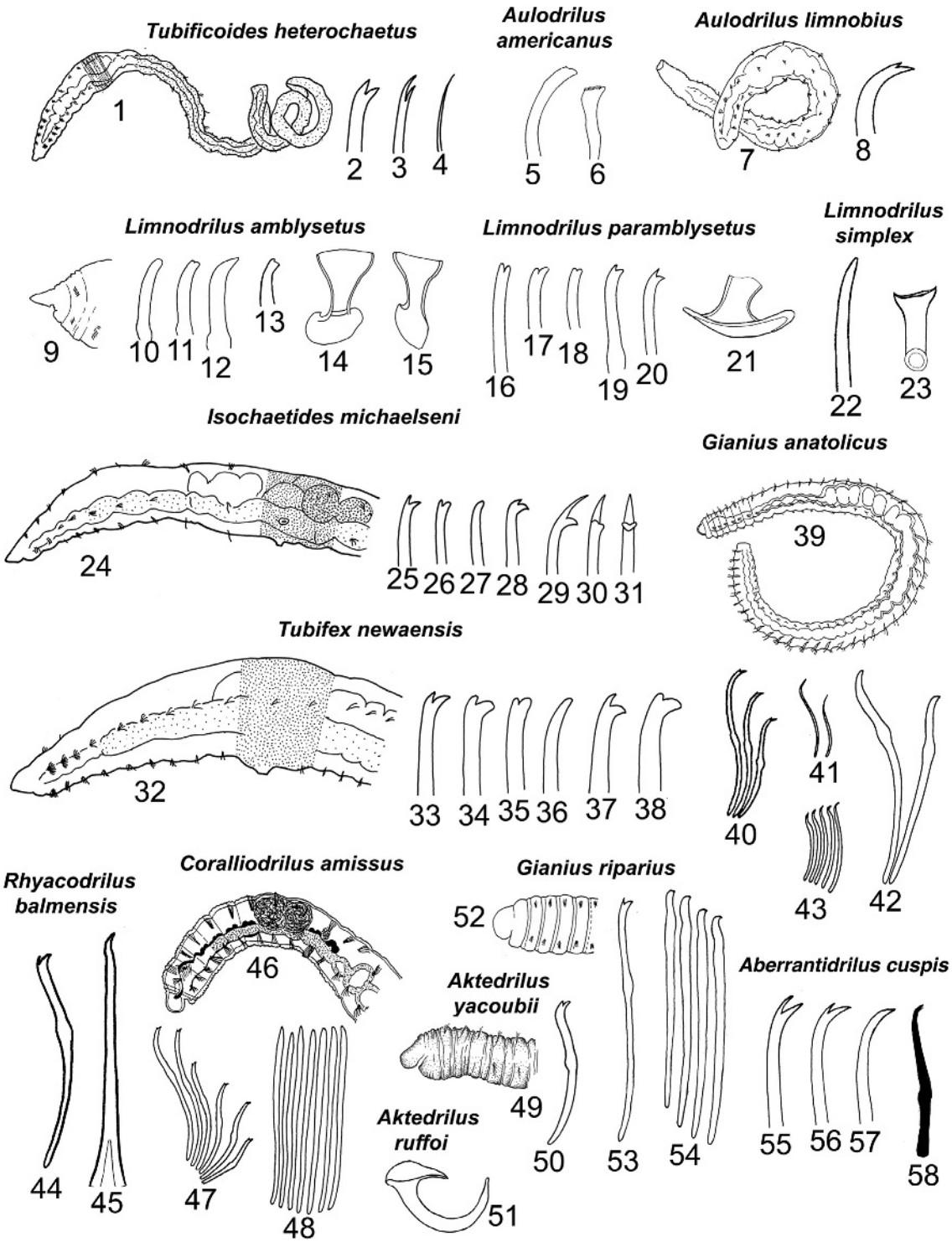


FIGURE 12.17 Tubificidae VII: (1–4): *Tubificoides heterochaetus*: (1) general view of sexually mature specimen, (2) anterior chaeta, (3) chaeta from midbody, (4) posterior chaeta; (5, 6): *Aulodrilus americanus:* (5) anterior chaeta, (6) chaeta from midbody; (7, 8): *Aulodrilus limnobius*: (7) general view, (8) chaeta; (9–15): *Limnodrilus amblysetus*: (9) anterior end, (10–12): anterior chaetae, (13) posterior chaeta, (14, 15) penis sheaths; (16–21): *Limnodrilus paramblysetus*: (16–19): anterior chaetae, (20) posterior chaeta, (21) penis sheath; (22, 23): *Limnodrilus simplex*: (22) chaeta, (23) penis sheath; (24–31): *Isochaetides michaelseni*: (24) forebody of sexually mature specimen with clitellum, (25–27) anterior chaetae, (28) posterior chaeta, (29–31): genital chaetae; (32–38): *Tubifex newaensis*: (32) forebody of sexually mature specimen with clitellum; (33–36): anterior chaetae; (37, 38) posterior chaetae; (39–42): *Gianius anatolicus*: (39) general view, (40) anterior ventral bundle, (41) posterior ventral bundle, (42) posterior dorsal bundle; (43) penial bundle; (44, 45) *Rhyacodrilus balmensis*: (44) ordinary chaeta, (45) penial chaeta; (46–48): *Coralliodrilus amissus*: (46) forebody of sexually mature specimen, (47) bundle of ordinary chaetae, (48) penial bundle; (49, 50) *Aktedrilus yacoubii*: (49) anterior end, (50) chaeta; (51): *Aktedrilus ruffoi*, penis sheath; (52–54): *Gianius riparius*: (52) anterior end, (53) ordinary chaeta, (54) penial bundle; (55–58): *Aberrantidrilus cuspis*: (55) anterior chaeta, (56, 57) posterior dorsal chaetae, (58) penial chaeta.

73(72) II with chaetae simple-pointed in ventral, sometimes also dorsal bundles; remaining segments with shorter upper tooth, 3−5 (six) anteriorly and 2−3 in postclitellar bundles; XI without ventral chaetae; male pore in XI single, mid-ventral, as is spermathecal pore in X; small coelomocytes abundant; VI−X with dilated transverse blood vessels; L = 15−70 mm; mostly in polluted water ..... ***Monopylephorus*** [in part; **p. 427**]

73′ Chaetae in anterior segments 3−4 per bundle and simple-pointed, posteriorly 1−2, with small upper tooth (larger chaetal numbers, 8−15, are known in Nearctic); atria with numerous small prostate glands..... *Telmatodrilus vejdovskyi* Eisen, 1879 [China: Yangtze River. Nearctic]

74(70) Most chaetae, at least in anterior bundles, with shorter and thinner upper tooth 75

74′ Chaetae at least in anterior bundles with equal teeth or upper tooth longer (although often thinner) 87

75(74) Length mostly >10 mm, living in surface waters; atria with solid prostate gland 76

75′ Length mostly <10 mm long, living mostly in groundwater, caves, and springs; atria equipped mostly with two prostate glands, more seldom single, or diffuse prostate tissue 80

76(75) No modified genital chaetae 77

76′ Single modified genital chaetae in ventral bundles of IX, X, and XII, with upper tooth length ≥ twice as low, lower laterally dilated; XI male pores without ventral chaetae; ordinary chaetae in anterior bundles 3−7, with shorter upper tooth, sometimes both teeth worn; posteriorly chaetae number and difference in chaetal length decreasing; L = 25−33 mm (Fig. 12.17(24−31)) ..... ***Isochaetides*** [in part; **p. 422**]

77(76) Penis sheaths absent 78

77′ Penis sheaths present ..... ***Limnodrilus*** [in part; **p. 430**]

78(76) Smaller worms, reproducing mostly by architomy (fragmentation); sexually mature reproductive system is usually shifted anteriorly or posteriorly from usual position 79

78′ Relatively large tubificid, 1−3 mm thick; reproduction exclusively sexual; male pores always in XI; chaetae with shorter upper tooth, teeth often worn; anterior bundles 3−8 per bundle; posteriorly the chaetal number and teeth difference decreasing; L = 45−90 mm; sandy large rivers (Fig. 12.17(32−38)) ..... ***Tubifex*** [in part; **p. 412**]

79(78) Male pores may lie in X, XI, XII, XIII, or XV, with spermathecal pores in previous segment; anterior chaetae 3−7 per bundle, only 1−2 ventrally in genital segments; posteriorly 2−4; chaetae teeth equal or upper tooth slightly shorter, usually thinner; dissepiments 3/4−10/11 (when male pores in XII) thickened; L = ∼20−25 mm ..... ***Potamothrix*** [in part; **p. 419**]

79′ Mature individuals (seldom occur) with male pores in VIII; clitellum beginning in VII; chaetae bifid with much shorter upper tooth, 5−10 per bundle; chaetae distally often dilated, forming lateral "wings"; unsegmented tail acting as respiratory organ; L = 10−15 mm (Fig. 12.17(7, 8)) ..... ***Aulodrilus*** [in part; **p. 417**]

80(75) Penial chaetae not hollow, or modified genital chaetae lacking; prostate glands solid 81

80′ XI penial chaetae with thickened, hollow proximal end and simple, fine, slightly hooked, converging tips, by 6−7; ordinary anterior bundle chaetae 2−5, posteriorly 1−3, with upper tooth shorter, thinner; atria with diffuse prostate tissue cover; large coelomocytes abundant; L = ∼3 mm; groundwater (Fig. 12.17(44, 45))..... ***Rhyacodrilus*** [in part; **p. 423**]

81(80) No penis sheaths; spermathecae paired, with ventral or lateral pores 82

81′ Conical penis sheath present; no ventral chaetae in XI; single spermatheca in X with dorsal pore. Coelomocytes present ..... ***Aktedrilus*** **[p. 431]**

82(81) Modified penial chaetae at male pores present 83

82′ No modified genital chaetae; ordinary chaetae at male pores in XI; chaetae with upper tooth shorter than lower, 3−4 in anterior and 2−3 in posterior segments; male pores on porophores; L = ?; groundwater ..... ***Gianius*** [in part; **p. 431**] [France]

83(82) Penial chaetae several per bundle; X with spermathecal pores before male pores 84

83′ Penial chaetae single, directed anteriad; XII with spermathecal pores after male pores, in XII; groundwater ..... ***Aberrantidrilus*** **[p. 432]**

84(83) All penial chaetae simple-pointed 85

84′ At least some penial chaetae bifid ..... ***Gianius*** [in part; **p. 431**]

85(84) Prostate glands present, 1−2 per atrium 86

85′ Atria without prostate glands; XI penial bundles consisting of 4−7 parallel, straight chaetae with distal nodulus and simple obtuse, slightly curved tip; ordinary chaetae 3−7 per bundle, bifid with short upper tooth; midgut widening only behind clitellum; L = 2.5−3 mm (Fig. 12.17(46−48))..... *Coralliodrilus amissus* Arslan, Timm, & Erséus, 2007 [Turkey]

86(85) Distal portion of atria modified into long eversible pseudopenis with winding lumen when retracted ..... ***Spiridion*** **[p. 432]**

86′ Atria with short and thin efferent duct. Groundwater ..... ***Gianius*** [in part; **p. 431**]

87(74) Prostomium without sensory pit 88

87′ Prolonged prostomium dorsally bears a sensory pit lined with thickened epithelium; large coelomocytes abundant ..... ***Bothrioneurum*** **[p. 432]**

88(87) Grooved genital spermathecal chaetae present in X or also in some neighboring segments 89

88′ Spermathecal chaetae bifid or lacking, not modified; blunt penial chaetae or penis sheaths present or lacking 95

89(88) Grooved genital chaetae only in X, or in X and XI 90

89′ Genital chaetae of spermathecal type, with narrow grooved distal portion, 1−2 in IX, X (at spermathecal pores), and XII; if two per bundle, then one with strongly curved and one with almost straight proximal end; these chaetae hidden in three pairs of glandular tubercles, respectively; ordinary chaetae in anterior dorsal bundles 3−6, in ventral bundles 4−7, in posterior bundles (one) 2−3 (four) bifid chaetae, all of similar shape, with upper tooth thicker and several times as long as lower; no ventral chaetae in XI; both atrial ducts opening in the unpaired median porophore in XI; L = 12−24 mm (Fig. 12.18(5−8)) ..... *Protuberodrilus tourenqui* Giani & Martínez-Ansemil, 1979 [Spain]

90(89) Grooved genital (spermathecal) chaetae only in X but not in XI 91

90′ Grooved genital chaetae of spermathecal type both in X and XI, single, with narrow distal portion, sitting in large fungiform chaetal glands; XI with bundles of 3−6 straight penial chaetae with short teeth; ordinary chaetae similar, with blunt teeth, in forebody 3−5 (six) per bundle, with longer upper tooth, posteriorly (one) two, with teeth becoming equal; L = ?; groundwater ..... ***Krenedrilus*** [in part; **p. 417**] [Spain]

91(90) Grooved spermathecal chaetae in X, modified (blunt or bifid penial) or unmodified ventral chaetae in XI 92

91′ Grooved spermathecal chaetae in X, penis sheaths (and mostly no ventral chaetae) in XI 93

92(91) X spermathecal chaetae single (seldom two), with narrow, acute distal portion; XI penial chaetae 2−4 per bundle, almost straight, blunt or with thicker and strongly curved upper tooth; ordinary chaetae in anterior bundles 3−7, posteriorly 2−6, with upper tooth length 2−3 times lower, difference decreasing posteriorly; dorsal chaetae of XI may be enlarged, with particularly long and wide upper tooth; large coelomocytes abundant; L = 11−13 mm (Fig. 12.18(9−16)) ..... ***Rhyacodrilus*** [in part; **p. 423**]

92′ Bifid chaetae or no chaetae (but no penis sheaths) at male pores in XI; no large coelomocytes ..... ***Potamothrix*** [in part; **p. 419**]

93(91) Penis sheaths not fungiform 94

93′ Penis sheaths in XI thick-walled, length = width, with funicular proximal and fungiform distal end; X often with single thin spermathecal chaetae with fine groove distally; ordinary chaetae 2−6 per bundle, with equal short teeth; L = 6−8 mm (Fig. 12.18(31−35)) ..... ***Peipsidrilus*** [in part; **p. 429**]

94(93) Penis sheaths consisting of a circular proximal part and unilateral palaform distal appendage; X may have single modified spermathecal chaetae, thin, straight, with proximal end bent, sitting in large gland, distal half finely grooved, or X instead may have a bundle of ordinary chaetae, or no ventral chaetae; ordinary chaetae bifid with slightly thinner, longer upper tooth, 3−10 in anterior and 2−4 in posterior segments; XI near male pores usually two short bifid chaetae; small "hearts" in VIII; L = 10−28 mm (Fig. 12.18(36−39)) ..... *Lamadrilus sorosi* Timm, 1998 [Russia: Lake Taimyr in Siberia]

94′ Penis sheaths thin-walled, symmetrical, without distal appendage ..... ***Isochaetides*** [in part; **p. 422**]

95(88) No modified spermathecal chaetae 96

95′ Bifid spermathecal chaetae in X (or also in IX and XII), blunt penial chaetae in XI; large coelomocytes abundant ..... ***Rhyacodrilus*** [in part; **p. 423**]

96(95) Penial chaetae present at male pores; no penis sheaths; large coelomocytes abundant 97

96′ No modified penial chaetae; penis sheaths can be present or lacking 100

97(96) Several blunt penial chaetae per bundle at male pores 98

97′ XI male pores with single, very large, falciform penial chaetae; all other chaetae with upper tooth length twice as low, 2−6 in anterior bundles and 1−2 posteriorly; abundant large coelomocytes present; living worm white; L = 8−10 mm; groundwater, springs, clean lakes, terrestrial soil (Fig. 12.18(44−46)) ..... ***Rhyacodrilus*** [in part; **p. 423**]

98(97) Both ordinary and penial chaetae ~10 per bundle 99

98′ Chaetae less numerous, 2−8 per bundle ..... ***Rhyacodrilus*** [in part; **p. 423**]

99(98) Ordinary chaetae up to 10 per bundle, uniformly pectinate, with longer upper tooth and short intermediate denticles or web; penial chaetae up to 10 per bundle but simple-pointed; prostomium small, acute; body wall and dissepiments very musculous; L = 30−65 mm ..... *Hrabeus korotneffi* (Michaelsen, 1905) [Russia: Lake Baikal, Angara and Enisej Rivers]

99′ Several blunt penial chaetae per bundle at male pores; anterior segments 10−13 chaetae, tooth length variable within a bundle; penial chaetae 9−10, with teeth variously rudimentary; L ≥ 10 mm ..... ***Rhyacodrilus*** [in part; **p. 423**]

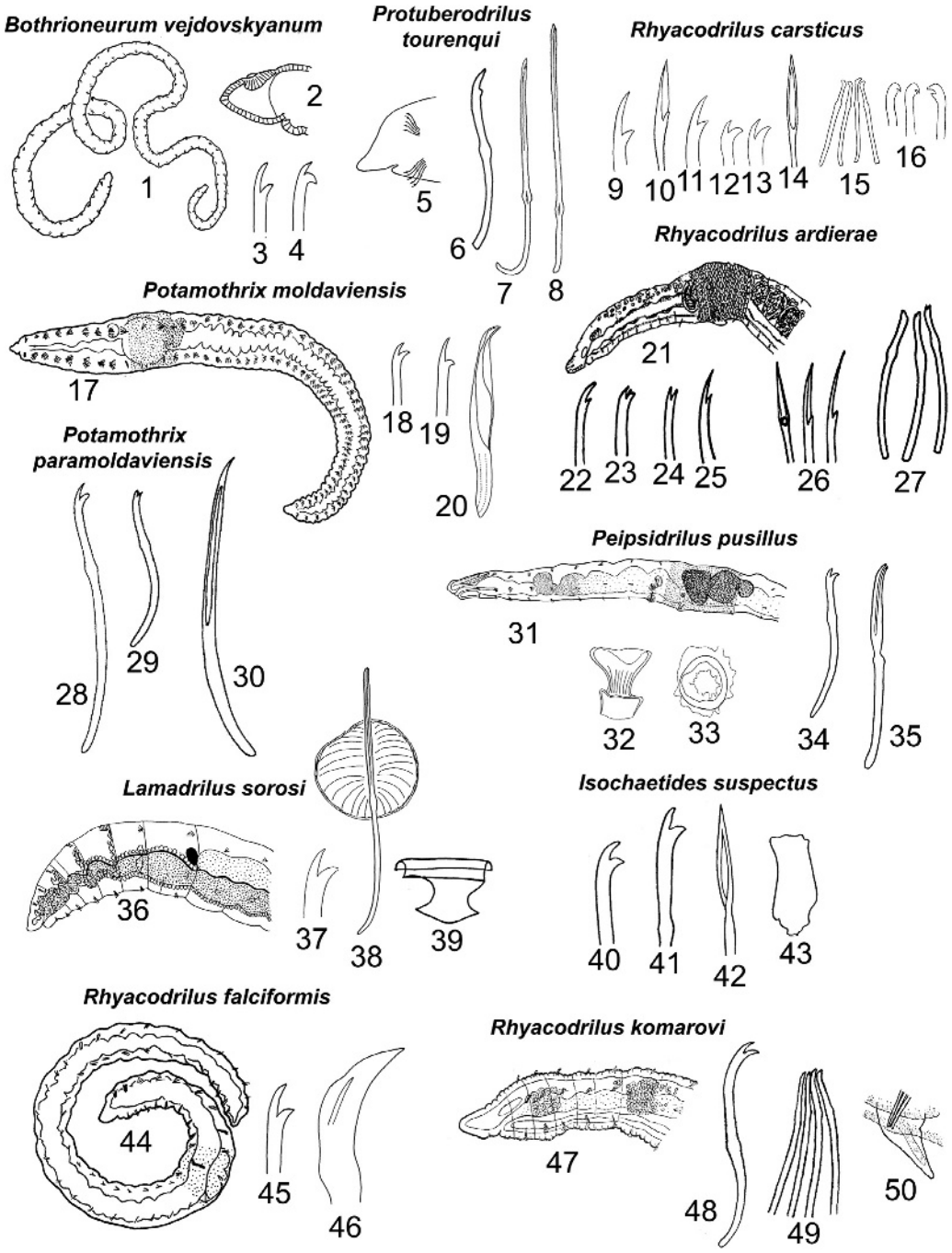


FIGURE 12.18 Tubificidae VIII: (1–4): *Bothrioneurum vejdovskyanum*: (1) general view, (2) anterior end with sensory pit, (3) anterior chaeta, (4) posterior chaeta; (5–8): *Protuberodrilus tourenqui*: (5) anterior end, (6) ordinary chaeta, (7, 8) genital chaeta; (9–16): *Rhyacodrilus carsticus*: (9) ordinary anterior chaeta, (10) modified dorsal chaeta from XI, (11–13): posterior chaetae, (14) spermathecal chaeta, (15) penial bundle, (16) penial chaetae; (17–20): *Potamothrix moldaviensis*: (17) general view of sexually mature specimen with clitellum, (18) ordinary chaeta, (19) penial chaeta, (20) spermathecal chaeta; (21–27): *Rhyacodrilus ardierae*: (21) forebody of sexually mature specimen with clitellum, (22) anterior ventral chaeta, (23) ventral chaeta from midbody, (24) anterior dorsal chaeta, (25) posterior chaeta, (26) three aspects of spermathecal chaeta, (27) penial bundle; (28–30): *Potamothrix paramoldaviensis:* (28) ordinary chaeta, (29) penial(?) chaeta, (30) spermathecal chaeta; (31–35): *Peipsidrilus pusillus*: (31) forebody of sexually mature specimen with clitellum, (32) penis sheath in lateral view, (33) penis sheath in terminal view, (34) ordinary chaeta, (35) spermathecal chaeta; (36–39): *Lamadrilus sorosi*: (36) anterior end, (37) ordinary chaeta, (38) spermathecal chaeta with gland, (39) penis sheath; (40–43): *Isochaetides suspectus*: (40) ventral chaeta, (41) dorsal chaeta, (42) spermathecal chaeta, (43) penis sheath; (44–46): *Rhyacodrilus falciformis*: (44) general view of sexually mature specimen with clitellum, (45) ordinary chaeta, (46) penial chaeta; (47–50): *Rhyacodrilus komarovi*: (47) anterior end, (48) ordinary chaeta, (49) penial bundle, (50) protruded penis with penial bundle.

100(96) Penis sheaths present; no ventral chaetae at male pores in XI 101

100′ Penial sheaths lacking 106

101(100) No enlarged chaetae 102

101′ Chaetae 1−4, mostly two in anterior bundles, 1−2 and much smaller posteriorly, with short equal long teeth; IV−X ventral chaetae extraordinarily large, blunt teeth; esophagus chloragogen tissue beginning in VI; penis sheaths very short, thick-walled,spadeform with funicular proximal base and asymmetrically hooded (with lateral appendage) or rounded triangular lamelliform distal end; L = 80−130 mm (Fig. 12.19(1−5)) ..... ***Limnodrilus*** [in part; **p. 430**]

102(101) Anterior chaetae with teeth equal or upper tooth slightly longer but not bent at right angle 103

102′ II−IV anterior most chaetae 3−8 per bundle, upper tooth thicker, length ≥ twice as low, bent nearly 90°; teeth becoming gradually equal in subsequent segments; esophagus chloragogen tissue beginning in VI; body tough, tail long and smooth, prolonged segments bearing transverse yellow stripes; penis sheaths small, short cylindrical, length ≥ four times maximum width; L = 35−70 mm (Fig. 12.19(6−11)) ..... ***Limnodrilus*** [in part; **p. 430**]

103(102) Penis sheaths almost cylindrical, gradually narrowing toward distal end 104

103′ Penis sheaths funicular with sharp blind distal end, or truncate conical 105

104(103) Penis sheaths with distinct wall, with dilatation or appendage distally; posterior chaetae fewer and usually with equal long teeth ..... ***Limnodrilus*** [in part; **p. 430**]

104′ Penis sheaths very thin-walled, cylindrical, length five times width; chaetae in anterior bundles 3−4 per bundle, with distal tooth slightly longer, thinner; posteriorly 2−3, with distal tooth shorter; esophagus chloragogen tissue scarce in V, well developed in VI; "hearts" in VIII, beginning dorsally in VII and ending ventrally in IX; male duct short, without prostate gland; L = 10−16 mm ..... *Chenidrilus asiaticus* (Chen, 1940) emend. Liang & Xie, 1997 [China]

105(103) Penial sheaths short, truncated conical; anterior bundles chaetae 4−7, bifid with larger upper tooth; individuals with occasional hair chaetae are described from brackish water in North America; L = 12−20 mm ..... ***Ilyodrilus*** [in part; **p. 428**] [Turkey(?). Nearctic. Neotropics]

105′ Penial sheaths thin-walled, funicular, proximal end dilating, main part cylindrical, distal end acute, blind, with lateral external aperture ..... ***Tasserkidrilus*** [in part; **p. 429**]

106(100) Male pores paired, accompanied with ordinary bifid chaetae 107

106′ XI male pore and X spermathecal pore single and midventral; small coelomocytes very abundant; chaetae bifid with sharp equal teeth or upper tooth slightly longer; older chaetae teeth may be worn; anterior bundles with 3−6, posterior ones with 2−4 chaetae; no ventral chaetae in XI; L = 10−60 mm (Fig. 12.19(41−44)) ..... ***Monopylephorus*** [in part; **p. 427**]

107(106) Several bifid chaetae per bundle in II and in subsequent segments 108

107′ All bundles of II single bifid chaetae, longer and thicker than rest, upper tooth thinner, slightly shorter than lower; from III, 2−3 bifid chaetae per bundle, with slightly longer upper tooth; hindbody bifids thicker, with equal teeth; loops of long transverse blood vessels tightly packed in III−V; L < 17 mm (Fig. 12.19(37−40)) ..... *Tubificidarum hrabei* Karaman, 1973 [Albania/Montenegro: Lake Skadar]

108(107) Anteclitellar dissepiments not thickened; midbody chaetae upper tooth not longer than in anterior segments 109

108′ Dissepiments 3/4−10/11 thickened; chaetae 3−6 per bundle but only 2−3 ventrally in X and 1−2 in XI; upper tooth longer and thinner than lower, the longest (by two times) in midbody; teeth tips often rounded; spermatozeugmata with one end expanded and the most part caudiform; L = 20−30 mm; estuarine ..... ***Potamothrix*** [in part; **p. 419**]

109(108) Anterior chaetae 6−8 (11) per bundle, teeth blunt, upper one slightly longer; posteriorly chaetae three, mostly with shorter upper tooth; small penis in very long sac, without sheath; spermatozeugmata scarce (1−2), pyriform; L = 20−42 ..... ***Isochaetides*** [in part; **p. 422**]

109′ Chaetae 4−5 per bundle, with slightly longer upper tooth in anterior segments, 2−3 and with subequal teeth posteriorly; L = 10−18 mm ..... ***Tubifex*** [in part; **p. 412**]

Oligochaeta: Tubificida: Tubificidae: *Troglodrilus*: Species

1 Spermathecal vestibule wide and bulbous; penial sheath with several longitudinal folds; L = 4.5−5 mm; groundwater (Fig. 12.11(1−5)) ..... *Troglodrilus galarzai* (Giani & Rodriguez, 1988) [France]

1′ Spermathecal vestibule elongated; penial sheath smooth; L = 4.5−5 mm; groundwater *Troglodrilus jugeti* Achurra, des Châtelliers & ..... Rodriguez, 2012 [Spain]

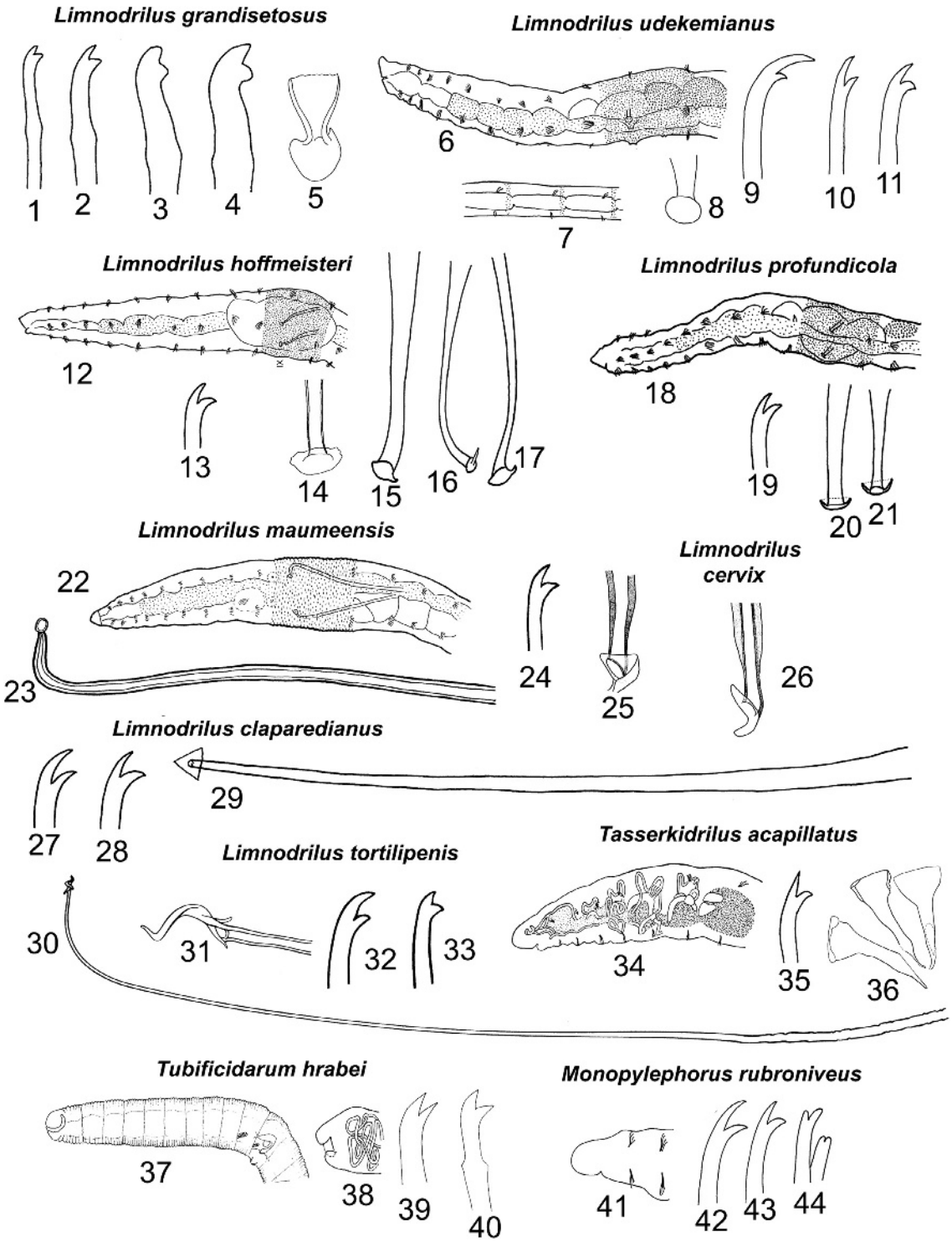


FIGURE 12.19 Tubificidae IX: (1–5): *Limnodrilus grandisetosus*: (1, 2) usual chaetae, (3, 4): enlarged ventral chaetae from IV–X, (5) penis sheath; (6–11): *Limnodrilus udekemianus*: (6) forebody of sexually mature specimen with clitellum, (7) fragment of tail with pigment stripes, (8) penis sheath, (9) chaeta from II, (10) intermediate chaeta from a subsequent segment, (11) posterior chaeta; (12–17): *Limnodrilus hoffmeisteri*: (12) forebody of sexually mature specimen with clitellum, (13) chaeta, (14) distal end of a "plat-topped" penis sheath, (15–17): typical penis sheaths; (18–21): *Limnodrilus profundicola*: (18) forebody of sexually mature specimen with clitellum, (19) chaeta, (20, 21) penis sheaths; (22–25): *Limnodrilus maumeensis*: (22) forebody of sexually mature specimen with clitellum, (23) penis sheath, (24) chaeta, (25) distal end of penis sheath; (26): *Limnodrilus cervix*, distal end of penis sheath; (27–29): *Limnodrilus claparedianus*: (27) chaeta from II, (28) posterior chaeta, (29) penis sheath; (30–33): *Limnodrilus tortilipenis*: (30) penis sheath, (31) distal end of penis sheath, (32) anterior chaeta, (33) posterior chaeta; (34–36): *Tasserkidrilus acapillatus*: (34) anterior end, (35) chaeta, (36) penis sheaths; (37–40): *Tubificidarum hrabei*: (37) forebody of sexually mature specimen with clitellum, (38) anterior end, (39) anterior chaeta, (40) posterior chaeta; (41–44): *Monopylephorus rubroniveus*: (41) anterior end, (42–44): chaetae.

Oligochaeta: Tubificida: Tubificidae: *Tubifex*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent 13

2(1) Body surface smooth, more or less transparent. Penial sheaths present or lacking 3

2′ Body surface armored with dark secretory papillae, in 3−4 rings per segment, papillae can be shed, giving for a short time a smoother and more transparent appearance; anterior dorsal bundles with none to two hair and 2−3 pectinate chaetae, the latter with 4−5 distinct intermediate denticles as long as the teeth; posteriorly 1−2 hair and two pectinate chaetae, denticles by 2−3, disappearing in terminal segments; ventral chaetae three to five in II−III and simple-pointed; three in IV−VI, simple-pointed, enlarged and mostly hook-shaped; 3−5 chaetae beginning from VII, bifid with upper tooth almost as long as lower in anterior segments but becoming half as long posteriorly; ventral chaetae lacking at male pores in XI; no penial sheath; L = 4.5−5 mm; groundwater ..... *Tubifex pescei* (Dumnicka, 1980)
[southern Europe]

3(2) Penis sheaths present 4

3′ No penis sheaths; anterior dorsal bundles with 3−5 finely pilose hair chaetae and 3−7 pectinate chaetae with slightly longer upper tooth and 1−6 long, thin intermediate denticles; anterior ventral bundles with 4−6 chaetae sometimes pectinate, with one or several short intermediate denticles, upper tooth length 1.5−2 times lower; number of chaetae and difference in chaetal length gradually decreasing posteriorly, to one chaeta per bundle; XI penial chaetae 1−2, simple or (seldom) with reduced upper tooth; L = 15−24 mm (Fig. 12.13(45−49)) ..... *Tubifex nerthus* Michaelsen, 1908
[western Palaearctic. Nearctic]

4(3) Penis sheaths present 6

4′ No penis sheaths (sometimes cuticle of penis thickened, remembering penis sheath) 9

5(4) Penis sheaths cylindrical or ovoid 6

5′ Penis sheaths ovoid, distally narrower; no spermathecae; anterior dorsal bundles 2−3 pilose hair chaetae and three pectinates with slightly longer upper tooth and small intermediate denticles; posteriorly one hair and one bifid chaeta; anterior ventral bundles 3−5 bifid chaetae, posteriorly one per bundle, with considerably longer upper tooth; XI two ordinary bifids; spermathecae; two pairs of dilated lateral vessels ("hearts"), in IX and X; L = 6 mm ..... *Tubifex minor* Sokolskaja, 1961
[Russia: Amur River]

6(5) Hair chaetae less numerous, pectinate chaetae with rough intermediate denticles; penis sheaths without collar 6

6′ Anterior hair chaetae 4−7, postclitellar one per bundle; pectinate chaetae with diverging teeth and a film of fine intermediate denticles, 7−9 in anterior bundles and three in posterior ones; anterior ventral chaetae 7−11, with equally thick teeth, upper tooth longer; posteriorly 2−3, upper tooth longer and thinner; "hearts" in VIII; penis sheaths very small, tubular with symmetrical distal end and proximal collar; L = up to 25 mm ..... "*Tubifex*" *solitarius* (Semernoy, 1972), incertae sedis
[Russia: Transbaikalia]

7(6) Penis sheaths prolonged conical or funicular, length ~ three times proximal width; dorsal pectinates with rough intermediate denticles 7

7′ Penis sheaths short truncated conical or funicular, with distal end oblique; dorsal chaetae intermediate denticles small or lacking; penis sheaths about as long as wide; hair chaetae smooth, none to one; pectinates 3−4 in anterior segments, with upper tooth slightly longer than lower, with 2−3 intermediate teeth; posteriorly 1−3, with equally long teeth and with 2−3 intermediate teeth; ventral chaetae with longer upper tooth, 4−5 in anterior bundles and 2−3 posteriorly; L = 4−5 mm (Fig. 12.15(43−46)) ..... "*Tubifex*" *conicus* He, Cui & Wang, 2012, incertae sedis
[China: Lake Yamzho Yumco in Tibet]

7(6) Spermathecae absent; anterior dorsal bundle hair chaetae 2−3, finely pilose or serrated; pectinate chaetae 2−3, with two equal obtuse teeth and several equal intermediate denticles forming a continous membrane; gradually replaced with ordinary bifids with longer upper tooth caudally; anterior ventral chaetae 3−5, upper tooth length two times; all chaetae decreasing to 1−2 caudally while difference between bifids teeth decreases; two pairs of "hearts", in VIII and IX; L= 8−12 mm (Fig. 12.15(34−37)) ..... "*Tubifex*" *montanus montanus* Kowalewski, 1919, incertae sedis
[central Europe, Turkey]

7′ Spermathecae present, sperm not arranged as spermatozeugmata; hair chaetae serrated, 1−2 in anterior dorsal bundles and one in midbody; pectinates 3−4, with equal teeth and 3−4 rough intermediate denticles, posteriorly with only one denticle attached to lower tooth; ventral bundles anteriorly (three) 4−6 chaetae with longer upper tooth; posteriorly the ventral chaetae number decreases from 3−4 (five) to 2−3 (four) while upper tooth becomes shorter; vas deferens uniformly ciliated; L = 8−10 mm ..... "*Tubifex*" *montanus parvus* Giani, Martínez-Ansemil & Brinkhurst, 1984, incertae sedis
[Lebanon]

8(3) Bifid chaetae at least in most anterior bundles with equal teeth, or the upper tooth longer 9

8′ Bifid chaetae (but not always pectinates if present) with upper tooth shorter; ventral chaetae thin, with slightly shorter upper tooth, anteriorly 2−6, posteriorly two; anterior dorsal bundles with 1−2 thin hair chaetae and 1−4 pectinates, the latter with equally long teeth and 1−3 intermediate denticles; segments extended, the thin body often spirally contorted in fixed specimens; L = 7−12 mm (Fig. 12.16(16−18)) ..... *Tubifex smirnowi* Lastočkin, 1927
[Palaearctic]

9(8) Male ducts present, spermathecae usually present but seldom lacking 10

9′ Male ducts and spermathecae lacking (apparently parthenogenetic), eggs present; anterior dorsal bundles none to four pilose hair chaetae and 1−4 pectinates with obtuse teeth and 3−6 long intermediate denticles; anterior ventral chaetae 2−5 per bundle, mostly with longer upper tooth; XI usually a single bifid chaeta; posteriorly bifids less in number and with equal tooth; two pairs of "hearts" in VII and VIII; L = 7−10 mm ..... "*Tubifex*" *pomoricus* Timm, 1978, incertae sedis
[Russia: Kola Peninsula; The Netherlands]

10(9) Spermathecae, when present, smaller, usually limited to X 11

10′ Spermathecae with dorsolateral openings in X, their large ampullae reaching in opposite directions, one into IX and the other far backward, sometimes to XV; anterior dorsal bundles (none) 1−3 (four), in posterior ones none to two hair chaetae; anterior pectinate chaetae by 2−4 (five), with equal length and 2−3 fine intermediate denticles of same length; posteriorly gradually replaced with 2−3 bifid chaetae with larger lower tooth; anterior ventral bundles (two) 3−4 (five) bifid chaetae with slightly longer and thinner upper tooth; posteriorly 2−3 (four) chaetae with equal teeth, the lower tooth thicker; XI male pores (two) three (four) bifid chaetae; penes relatively long, cylindrical, retracted, without cuticular sheath; L = 6−12 mm (Fig. 12.16(19−21)) ..... *Tubifex acuticularis* Martínez-Ansemil & Giani, 1983
[Near East]

12(11) Anterior dorsal bundles 1−6 very finely pilose hair chaetae and 2−5 pectinates with equal main teeth and shorter but distinct intermediate teeth; anterior ventral chaetae 3−6 per bundle, with slightly longer upper tooth; posterior segments dorsal and ventral bifids two, with upper tooth shorter and thinner, lower one stout and curved; dorsal bundles at least in midbody single hair chaetae; XI male pores 1−2 small bifids; pair of thickened transverse blood vessels, or "hearts," in VIII; vasa deferentia bipartite, with thicker distal portion, appearing finely "segmented"; penial sacs rough, flexible cuticle sometimes confused with a penis sheath; L = 10−100 mm (Fig. 12.16(26−31)) ..... *Tubifex tubifex* (Müller, 1774)
[cosmopolitan]

12′ Hair chaetae beginning in VII−VIII, one per bundle, or absent; anterior dorsal bundles 3−8 pectinate chaetae with slightly longer upper tooth and only 1−2 small intermediate denticles attached to lower tooth; anterior ventral bundles 3−6 bifids (or pectinates) with longer upper tooth and small intermediate denticles as in dorsal ones; posteriorly 2−3 bifids, caudally only one, with equal teeth but lower tooth thicker; genital region with unmodified ventral chaetae; L = 17−30 mm; slightly brackish water, may be an ecological form of the previous species ..... *Tubifex bergi* Hrabě, 1935
[central Asia; Transcaucasia; Turkey]

13(1) Chaetae 4−5 per bundle, with slightly longer upper tooth in anterior segments, 2−3 and with subequal teeth posteriorly; L = 10−18 mm; anatomically similar to some ecological forms of *Tubifex tubifex* ..... *Tubifex blanchardi* Vejdovský, 1891
[northern Africa, southern Europe]

13′ Most chaetae, at least in anterior bundles, with shorter and thinner upper tooth; reproduction exclusively sexual; male pores always in XI; chaetae with teeth often worn; anterior bundles 3−8 per bundle; posteriorly the chaetae number and length difference decreasing; relatively large tubificid, 1−3 mm thick; L = 45−90 mm; sandy large rivers and lakes (Fig. 12.17(32−38)) ..... *Tubifex newaensis* (Michaelsen, 1903)
[western Palaearctic]

Oligochaeta: Tubificida: Tubificidae: *Baikalodrilus*: Species (excluding Lake Baikal)

1 Body armored with high but separate dark papillae; II−IV dorsal bundles of 3−5 smooth hair chaetae with slightly hooked tip, and 3−4 sigmoid bifid chaetae (or pectinates with a single intermediate denticle), fewer in following segments; postclitellar bundles 2−3 hair chaetae and 1−2 fine, simple needle chaetae; II ventral chaetae 4−5 per bundle, III−IV 3−4, in V−VI 2−3, in VII−VIII 1−2, and posteriorly only one; foremost segments, II−IV(VI), both single-pointed and bifid chaetae with longer upper tooth; posteriorly only bifids, their length becoming equal, lower tooth thicker and curving; XI ventral chaetae lacking in mature individuals; L = 10−20 mm ..... *Baikalodrilus alienus* Timm, 1998
[Russia: Lake Taimyr in Siberia]

1′ Epidermal papillae small, dense, forming transverse rings caudally; anterior dorsal bundles with 2−4 hair and 2−4 pectinate chaetae, the latter with fine membrane or an intermediate denticle between equal, thin teeth; ventral bundles bifid chaetae only with slightly longer lower tooth; anterior bundles 3−4 per bundle, posterior ones two; L = ∼40 mm ..... *Baikalodrilus inflatus* (Michaelsen, 1901)
[Russia: Lake Baikal and dubious records from the vicinity]

Oligochaeta: Tubificida: Tubificidae: *Embolocephalus*: Species (excluding Lake Baikal)

1 Modified genital chaetae of "spermathecal type "(with grooved, spatulate or hollow distal portion) either in X, or X and XI (but can be lacking in some single individuals) 2

1′ No modified genital chaetae (bifid crotchets present or lacking at genital pores) in ventral bundles of II–III bifid and single simple-pointed chaetae, thinner than the rest, with obtuse tip; forebody ventral bundles four, posterior with two bifid chaetae, the upper tooth slightly longer in anterior bundles but considerably shorter and thinner in mid- and hindbody, teeth not strongly curved; dorsal bundles with 4–5 thick, pilose hair chaetae and 2–4 shorter than papillae, needle-shaped pectinate chaetae, with none to three very fine intermediate denticles; body armored with high brownish-red papillae, except clitellum and 4–5 last segments; light sensory papillae in two transverse rows per segment; L = 15–20 mm ..... *Embolocephalus chukotensis* (Morev, 1975)
[Russia: Chuckchi Peninsula]

2(1) Body armored with papillae and secretion consisting of foreign particles; ventral bundles with single-pointed chaetae (combined with bifids or without them) 3

2′ Body enclosed in a layer of secretion with adhering foreign particles, papillae only in clitellum and around male pores; anterior dorsal bundles with 3–5 hair chaetae and 2–3 small, narrowly pectinate chaetae with a web between teeth; posterior 2–3 hair and 1–2 pectinates; II–IX ventral chaetae 2–3, bifid with upper tooth longer than lower in anterior segments becoming subequal posteriorly; spermathecal chaetae not observed but a glandular sac opening into spermathecal duct; no ventral chaetae in IX in mature individuals; L = 70–80 mm. ..... *Embolocephalus nomurai* (Yamamoto & Okada, 1940)
[Japan: Lake Tazawa]

3(2) Hair chaetae maximum seven per bundle 4

3′ Body armored with secretory papillae of different size, covered with adhering foreign particles; largest papillae are arranged in a single transverse row per segment and simultaneously in 2–3 dorsal and two lateral longitudinal rows along body; additionally two transverse rows of light sensory papillae per segment; forebody dorsal bundles with 1–12, midbody to 16, hindbody 4–6 hair chaetae; additional, obscure short, fine needle chaetae with forked tip; forebody ventral chaetae two, one bifid; posteriorly only single simple-tipped crotchets; one modified spermathecal chaetae with hollow distal portion in X; no ventral chaetae at male pores in XI; L = 4–21 mm ..... *Embolocephalus stankovici* (Hrabě, 1931)
[Albania/Macedonia: Lake Ohrid]

4(3) Hindbody ventral chaetae not considerably larger than those of forebody 5

4′ Postclitellar ventral chaetae considerably larger and strongly curved 7

5(4) Bifid chaetae prevailing in ventral bundles; spermathecal chaetae (if known) straight, without lateral dilatation 6

5′ Body densely covered with dark secretory papillae, among them usually two transverse rows of slightly larger ones, and a row of light sensory papillae; dorsal bundles with 1–4 hair chaetae and one to four short bifids of obscure shape, concealed in the armor; ventral chaetae 1–2 per bundle, simple or simple plus bifids with reduced upper tooth, more curved posteriorly; spermathecal chaetae in X truncated, with a narrow alate dilatation; L = 18–50 mm (Fig. 12.11(19–21)) ..... *Embolocephalus velutinus* (Grube, 1879)
[Palaearctic]

6(5) Body densely armored with dark oval papillae larger in postclitellar region; preclitellar segments with light sensory papillae in two rows, hindbody only one row; dorsal bundles with 3–4 smooth, curved hair chaetae and 2–3 small pectinate chaetae with hardly visible thin intermediate denticles; hair chaetae two in posterior segments; forebody ventral chaetae 2–3 per bundle, in II–III one simple, the remainder with longer upper tooth; posterior ventral chaetae two, their teeth length becoming subequal; modified spermathecal chaetae in X, grooved, distal half dilated in proximal portion, apex thin, curved acute; L = ~20 mm ..... *Embolocephalus kurenkovi* (Sokolskaja, 1961)
[Russia: Kamchatka]

6′ Body densely covered with brown, high, oval papillae; anteriormost segments (up to IV) may bear smaller, colorless papillae; dorsal bundles with 1–3 hair chaetae, some finely pilose, and 1–3 tiny pectinate chaetae with 1–3 tiny, short intermediate denticles; ventral bundles of II with 1–2 sharp simple and 1–2 bifid chaetae, with upper tooth length twice as low; III ventral chaetae two, one simple the other bifid; IV–X bifid chaetae 2–3, teeth becoming equal; posterior chaetae one (two), thicker with shorter upper tooth and thicker lower tooth, not strongly sigmoid; no ventral chaetae on X and XI in clitellate individuals; reproductive organs not described; L = 13–36 mm ..... *Embolocephalus oregonensis* (Brinkhurst, 1965)
[Russia: western Siberia(?). Nearctic]

7(4) No white, tumid bands in forebody 8

7′ Body, including prostomium densely papillate, the papillae foliiform; segment II–IX with white and wide tumid band without papillae, less prominent ventrally; one or two rows of sensory papillae per segment, often disordered; anterior dorsal bundles with 3–7 curved, finely pilose hair chaetae and 3–6 pectinate chaetae with several intermediate denticles in their lyriform distal end; postclitellar dorsal bundles 1–4 hair and 1–4 pectinate chaetae; ventral chaetae 1–4, one simple the others bifid; II–VI(VIII) with much longer upper tooth; midbody one (two) bifid chaetae with both teeth subequally thick; chaetae become larger and more curved posteriorly, with upper tooth much thinner and shorter than lower; spermathecal chaetae long, thin and hollow, the right and left chaeta lying asymmetrically in X; ventral chaetae absent in XI of mature individuals; L ≤ 35 mm ..... *Embolocephalus yamaguchii* (Brinkhurst, 1971)
[Japan]

8(7) Body with dark oval papillae larger and sparser posteriorly; besides them 2−4 transverse rows of light sensory papillae per segment. Dorsal anteclitellar bundles with 3−7 stiff, curved, smooth or very finely pilose hair chaetae and 2−5 small pectinates with parallel teeth and several small intermediate denticles, without nodulus; 1−4 hair and 1−3 pectinate or bifid chaetae in postclitellar bundles; forebody ventral chaetae 2−3 per bundle, mostly bifid but in II or II−III(IV) accompanied with some simple chaetae; bifids upper tooth twice as long as lower; postclitellar ventral crotchets single, much thicker and more curved, with thicker and longer lower tooth diverging from upper at right or even obtuse angle; X single spermathecal chaetae with narrow, hollow distal portion in the spermathecal pore; XI ventral chaetae absent in mature individuals; L = 20−50 mm (Fig. 12.11(22−26)) ..... *Embolocephalus nikolskyi* (Lastočkin, 1953) [Asia. Nearctic(?)]

8′ Body with subequal, large secretory papillae; forebody dorsal bundles with 2−3 thick, curved hair chaetae and 2−3 aciculate (pectinate?) chaetae with two very thin teeth, decreasing in number gradually posteriorly, to one chaeta of each kind in hindbody; forebody ventral chaetae either two in every bundle, one simple and one with smaller upper tooth, or only a single simple chaeta; postclitellar bundles ventral chaetae single, much thicker, very strongly curved, with upper tooth reduced or lacking; mature individuals unknown; L = ∼20 mm..... *Embolocephalus cernosvitovi* (Hrabě, 1931) [Albania/Macedonia: Lake Ohrid]

Oligochaeta: Tubificida: Tubificidae: *Spirosperma*: Species

1 Body wall armored with secretory papillae 2

1′ Body armored with a layer of adhering particles, sometimes in transverse wrinkles (scarce small papillae can occur caudally) 3

2(1) Anterior dorsal bundles with ≤7 thick, curved hair chaetae and three to five very fine pectinate chaetae with parallel teeth; anterior ventral chaetae 2−5 per bundle, with upper tooth longer than lower; tail region dorsal and ventral bundles sparser and thicker, more curved bifid crotchets with particularly large and curved lower tooth; L = 15−40 mm (Fig. 12.11(10−13)) ..... *Spirosperma ferox* Eisen, 1879 [Holarctic]

2′ Anterior dorsal bundles with three hair and one needle chaetae; two hair chaetae and two needles in middle and posterior segments; anterior ventral chaetae five per bundle, three posteriorly, bifid with teeth equal, upper tooth thinner than lower; mature individuals unknown; L = 7 mm; clean streams ..... "*Spirosperma*" *nagarkotensis* Nesemann, 2007, incertae sedis [Nepal]

3(1) Armor relatively thin 4

3′ Body covered with a layer of mineral particles adhering to thick, transversely folded cuticle; anterior dorsal bundles with 4−5 short, thick hair chaetae and 2−3 pectinates with equal teeth and numerous intermediate denticles; number of dorsal chaetae decreasing in postclitellar segments; ventral chaetae in anterior bundles three, in midbody two, and in hindbody one per bundle; anterior chaetae relatively thin and with longer upper tooth; posterior the chaetae become gradually thicker and more curved, their upper tooth smaller and the lower tooth longer, much thicker and more curved; L = 12−16 mm ..... *Spirosperma scodraensis* (Hrabě, 1958) [Albania, Montenegro: Lake Shkodër]

4(3) Armor without papillae; Balkan Peninsula 5

4′ Armor almost without papillae (sometimes sparse papillae caudally) but finely granulated, ringed with dark stripes along transverse furrows, 2−3 per segment in forebody but up to 12−16 from VI−VIII; sensory papillae hardly distinguishable, two rows per segment in forebody but 3−4 per segment in hindbody; dorsal bundles with 3−7 long, curved, finely pilose hair chaetae and 2−4 thinner pectinate chaetae with distal end lyriform and 3−4 intermediate denticles; chaetae number may decrease posteriorly; ventral chaetae 3−6 in anterior bundles, thinnest in II, with longer upper tooth; from VII−VIII ventral chaetae become larger, with thicker lower tooth; posterior chaetae only (one) two per bundle, with thick, strongly curved lower and much smaller upper tooth; penis usually soft but equipped with thin, short cuticular sheath in f. *sachalinensis* Sokolskaja, 1964; L = 17−35 mm; ..... *Spirosperma apapillatus* (Lastočkin, 1953) [China, Japan, Russia]

5(4) Body covered with thin layer of adhering foreign particles; anterior dorsal bundles with 3−4 short, curved hair chaetae and 2−3 pectinate chaetae; pectinates with widely separated teeth, convex laterally, and 2−5 thick intermediate denticles; forebody ventral chaetae 1−2, posteriorly one per bundle, bifid, in anteriormost segments smaller and with subequal teeth, from VI−IX with reduced upper and very thick lower tooth; postclitellar ventral chaetae very strongly curved; ventral chaetae lacking in XI; L = ∼29 mm ..... *Spirosperma tenuis* (Hrabě, 1931) [Albania/Macedonia/Greece: Lake Ohrid and Lake Prespa]

5′ Body covered with thin layer of secretion; epidermis cells of different height forming several transverse rings per segment, furrows between latter dark due to adhering foreign particles; anterior dorsal bundles with 5−9 relatively short, thick, curved hair chaetae and 2−4 thinner pectinate chaetae; pectinates with thin, laterally convex teeth and 2−4 long, fine intermediate denticles; chaetal number decreasing posteriorly; forebody ventral chaetae 2−6, midbody 1−3, hindbody one per segment; anteriormost ventral chaetae with upper tooth length 1.5 times lower; posteriorly chaetae become gradually thicker and more curved, upper tooth smaller, but lower tooth thicker and strongly curved; ventral crotchets of XI bifid but smaller than remainder; L = 8−22 mm ..... *Spirosperma striatus* (Pop, 1977) [Romania]

Oligochaeta: Tubificida: Tubificidae: *Haber*: Species (excluding Lake Baikal)

1 Body surface armored: either with dark secretory papillae, with transverse rows of large epidermic glands or sensory papillae, or with fine transverse furrows incrusted with sticky secretion and foreign particles; armor often lacking on prostomium and on I–II, which can be retracted; armor can be shed, giving for a short time smoother and more transparent appearance; in most species no penial sheaths 2

1′ Body surface smooth, more or less transparent; penial sheaths present or lacking 3

2(1) Body covered with irregular transverse rows of fine secretory papillae; additionally, two rows of light-sensory papillae per segment; dorsal bundles with one (two) hair chaeta and one pectinate chaeta with 3–4 fine but long intermediate denticles; ventral bundles 1–3 (four) bifid chaetae with thin teeth, upper tooth length 2–2.5 times lower; L = 1.3–2.6 mm; groundwater (Fig. 12.11(27–31)) ..... *Haber turquinae* (Juget & Lafont, 1979)
[France]

2′ Papillae absent; fine transverse rows of glandular epidermis, encrusted with dark secretions and foreign particles; intersegmental furrows light and transparent; dorsal bundles 1–2 very finely pilose hair chaetae and 1–2 pectinate chaetae, with obtuse teeth and 2–8 intermediate denticles; ventral bundles 1–4 bifid chaetae with upper tooth twice as long in forebody, but with equal teeth posteriorly; IX and XI with single modified genital chaetae of spermathecal type, before spermathecal pores at male pores; in some individuals ventral chaetae of XI may be unmodified; spermathecal pores lateral; L = 10–12 mm (Fig. 12.11(32–37)) ..... *Haber speciosus* (Hrabě, 1931)
[Holarctic]

3(1) Dorsal hair chaetae scarce but very long, about 1 mm; bifid chaetae with much shorter upper tooth 4

3′ Dorsal hair chaetae not prolonged; bifid chaetae with teeth subequal or upper tooth longer; pectinate chaetae present in dorsal bundles 5

4(3) Dorsal hair chaetae only in some fore- and midbody bundles, single and length four times body diameter; bifid chaetae with shorter upper tooth, anterior dorsal bundles 3–5 and ventral bundles 3–4 (five, six), gradually decreasing to one in hindbody; modified genital chaetae may be lacking but a spermathecal type chaeta, grooved and acute, may occur in XI at male pore; body very thin; L = 20–25 mm, with maximum diameter only 0.2 mm ..... *Haber dojranensis* (Hrabě, 1958)
[Macedonia/Greece: Lake Dojran]

4′ Dorsal hair chaetae only in postclitellar region, one (two) per bundle, about 1 mm, thin and brittle; dorsal and ventral bundles bifid chaetae 3–7 and 3–8, respectively, with rudimentary upper tooth; modified genital spermathecal type chaetae both in X and XI, straight and grooved, small, hidden inside body wall; L = 38 mm ..... *Haber swirenkoi* (Lastočkin, 1937)
[Ukraine; Turkey]

5(3) Penes soft, without sheath 6

5′ Penis sheaths with proximal edge turned up; dorsal bundles mostly (one) 2–3 smooth hair chaetae and (one) 2–5 pectinate chaetae with equally long teeth and 1–2 delicate intermediate denticles; only one hair and 1–2 bifid, respectively, in tail region; ventral bundles mostly (one) 3–5 (six) but in tail region only 2–3, with slightly longer and thicker lower tooth; single spermathecal chaetae always present in X; similar modified chaetae in XI of some mature individuals while in the others only 1–2 ordinary bifids or no chaetae at male pores; L = 9–15 mm ..... *Haber pyrenaicus* (Juget & Giani, 1974)
[France, Spain]

6(5) Not more than two hair and four pectinate chaetae per bundle 7

6′ Dorsal hair chaetae 1–6 per bundle, very finely pilose; pectinate chaetae 1–7, with subequal teeth and a delicate plate formed by intermediate denticles; one hair and one pectinate chaeta in postclitellar bundles; anteclitellar ventral chaetae (two) 4–6, with teeth equal or upper tooth slightly longer; postclitellar ventral chaetae two, with equal teeth; spermathecal and male pores in X and XI with single genital chaetae, all similarly thin with grooved distal portion and slightly curved tip; L ≤ 23 mm (Fig. 12.12(6–10)) ..... *Haber amurensis* (Sokolskaja & Hrabě, 1969)
[southeastern Russia]

7(6) Anteriodorsal bundles with 1–2 hair and 1–2 (three) pectinate chaetae with long, acute teeth (the upper slightly longer than lower) and some fine intermediate denticles; posterior dorsal bundles with only one hair and one bifid chaeta with shorter and equally long teeth; anterior ventral bundles with 3–4 bifid chaetae, posteriorly 2–3; single modified genital spermathecal type chaetae in X and XI; groundwater ..... *Haber monfalconensis* (Hrabě, 1966)
[Italy]

7′ Hair chaetae 1–2; dorsal pectinate chaetae in forebody 3–4, with thin long teeth and up to six thin, slightly shorter intermediate denticles; postclitellum they are replaced by two bifid chaetae; ventral bundles 3–5 bifid chaetae with slightly shorter upper tooth; single modified genital spermathecal type chaetae in X and XI; no penial sheath but penis with thickened hypodermal walls; L = 10 mm ..... *Haber hubsugulensis* (Semernoy, 1980)
[Mongolia: Lake Hubsugul; Russia: Lake Baikal]

Oligochaeta: Tubificida: Tubificidae: *Krenedrilus*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent; grooved genital chaetae of spermathecal type both in X and XI, single, with narrow distal portion, sitting in large fungiform chaetal glands; XI with bundles of 3−6 straight penial chaetae with short teeth; ordinary chaetae similar, with blunt teeth, in forebody 3−5 (six) per bundle, with longer upper tooth, posteriorly (one) two, with teeth becoming equal; L = ?; groundwater .... *Krenedrilus ibericus* Giani, Erséus & Martínez-Ansemil, 1990 [Spain]

2(1) Typical "spermathecal" chaetae (sharp-tipped and with grooved, spoon-shaped or hollow distal portion, apparently functioning as syringe) present at spermathecal pores, in some species also (or only) at male pores..... 3

2′ No grooved or hollow "spermathecal"; two types of genital chaetae in XI, at each male pore a straight chaeta (seldom two) with slightly tumid, acute tip, equipped with a large gland, and a bundle of 3−10 simple penial chaetae with clavate, finely hooked distal end; X ventral chaetae unmodified, spermathecal pores dorsolateral; dorsal hair chaetae pilose, 3−5 in anterior and 1−3 in posterior segments; additionally relatively straight bifid chaetae with equal, divergent teeth, 2−4 in anterior and 1−3 in posterior bundles; anterior ventral bundles with 3−6 bifid chaetae, their teeth equally long, and 3−6 simple chaetae; only 3−6 bifid chaetae with shorter upper tooth, in posterior bundles; irregular spermatozeugmata and free spermatozoa in spermathecae; L = 3−6 mm (Fig. 12.13(20−26)) .... *Krenedrilus towadensis* Ohtaka, 2004 [Japan: Lake Towada]

3(2) Dorsal bundles with 1−3 hair chaetae 700−1400 μm long, and 1−4 pectinate chaetae with 2−3 intermediate denticles; anterior ventral bundles with 4−6 crotchets, some of them bifid with longer upper tooth and others simple-pointed; posterior bundles 2−3 chaetae with equal teeth; all chaetae with large glandular sacs; X and XI modified spermathecal type genital chaetae very long and narrow, with distal portion long, grooved, accompanied in XI by a bundle of slightly modified (penial), straight bifid chaetae; X with a single epidermal papilla between spermathecal pores; small worms (Fig. 12.12(11−16)); groundwater .... *Krenedrilus sergei* Giani, Erséus & Martínez-Ansemil, 1990 [France]

3′ Dorsal bundles with 2−3 (four) finely pilose hair chaetae and (one) two (three) bifid chaetae with fine equal teeth; ventral bundles 2−4 chaetae, some bifid with longer upper tooth and some simple; X and XI modified genital spermathecal type chaetae with grooved distal portion (in IX smaller) accompanied by a separate bundle of straight, bifid penial chaetae; stalked epidermal papilla between spermathecal pores in X; male pores bulged; small worms ..... *Krenedrilus realis* Martínez-Ansemil & Collado, 1996 [Spain]

Oligochaeta: Tubificida: Tubificidae: *Aulodrilus*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent 6

2 Modified genital chaetae present in sexually mature individuals 3

2′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals 4

3(2) Dorsal hair chaetae (none) 1−6 per bundle, short; anterior dorsal bifid chaetae 2−10, ventrally 3−11 per bundle, with reduced upper tooth (some ventral crotchets may appear simple); midbody from VII−IX, dorsal bifids are replaced with clavate "pectinates" with broad, rounded distal portion; at male pores one to two acute, grooved genital chaetae; L = 5−12 mm (Fig. 12.12(17−22)) .... *Aulodrilus pigueti* Kowalewski, 1914 [cosmopolitan]

3′ Dorsal hair chaetae (none) 1−2 per bundle, short; anterior dorsal bifid chaetae 3−7, with teeth equally long; midbody, from about VII pectinate chaetae with wide distal portion, main teeth and 2−3 (four) intermediate teeth subequal; male pores with 1−2 genital chaetae cupped, acute distally; L = 5−6.5 mm ..... *Aulodrilus pectinatus* Aiyer, 1928 [Asia. Oriental]

4(2) XI male pores with unmodified (usually bifid) ventral chaetae (seldom in VII or X) 5

4′ XI male pores without ventral chaetae; bifids not much thicker in the posterior segments, present in X and lacking in XI only; ventral chaetae 1−4, with conspicuously longer upper tooth; dorsal bundles with 1−4 smooth hair chaetae and 2−4 pectinates with subequal, slender teeth and 2−3 small intermediate denticles; L > 13 mm ..... *Aulodrilus apeniatus* Cui & Wang, 2009 [China: Lake Fuxian]

5(4) Dorsal bundles 2−8 hair chaetae and 5−10 bifid crotchets, the latter with short upper tooth split into many tiny denticles in a transverse row, giving chaeta a broken appearance; ventral bundles 5−11 bifids; similar bundles also at male pores in X; dark chloragogen tissue on esophagus in X only, wide midgut beginning in XI; L = 20−25 mm (Fig. 12.16(6, 7)) .... *Aulodrilus japonicus* Yamaguchi, 1953 [Palaearctic]

5′ Anterior dorsal bundles usually 6−8 hair chaetae and 6−9 bifid crotchets with shorter, entire upper tooth; anterior ventral bundles 8−17 similar bifids; crotchets distal portion immediately proximal to teeth often slightly dilated; the number of chaetae decreasing posteriorly; similar ventral chaetae at male pores in VII; dark chloragogen tissue on esophagus in VI−VII, wide midgut beginning in VIII; L = 14−40 mm (Fig. 12.16(1−5)) ..... *Aulodrilus pluriseta* (Piguet, 1906)
[Holarctic. Oriental. Australian]

6(1) Mature individuals (seldom occur) with male pores in VIII; clitellum beginning in VII; chaetae bifid with much shorter upper tooth, 5−10 per bundle; chaetae distally often dilated, forming lateral "wings", never palmate; L = 10−15 mm (Fig. 12.17(7, 8)) ..... *Aulodrilus limnobius* Bretscher, 1899
[cosmopolitan]

6′ Anteriormost bundles, both dorsal and ventral, with up to 10 chaetae, simple or with rudimentary upper tooth; from ~VI−X posteriorly chaetae becoming palmate, with numerous intermediate denticles forming together with short main teeth a broad lobe, mostly eight per bundle; similar chaetae, fewer in number, in hindbody, and ventrally in XI, at male pores (Fig. 12.17(5−6)) ..... *Aulodrilus americanus* Brinkhurst & Cook, 1966
[China, Japan (both single records). Nearctic]

Oligochaeta: Tubificida: Tubificidae: *Rhyacodriloides*: Species (without Endemics of Lake Baikal)

1 Hair chaetae 1(2) in preclitellar dorsal bundles, at least in II−III; bifid (with shorter upper tooth) and simple crotchets present, 1−8 in dorsal and 2−9 in ventral bundles; anteriormost and posteriormost bundles may consist of simple chaetae only; ventral chaetae bundles with large glands; ventral chaetae of X unmodified; XI at each male pore a genital spermathecal type chaeta slightly sigmoid, with narrow, grooved, acute distal portion, longer than proximal shaft, embedded in large setal gland and equipped with a large, prostata-like accessory gland; L = 1.7−2.3 mm; caves (Fig. 12.12(23)) ..... *Rhyacodriloides latinus* Martin, Martínez-Ansemil & Sambugar, 2010
[Italy, Slovenia]

1′ Hair chaetae 1(2) in II−VI(VII); bifid (with shorter upper tooth) and simple crotchets present both in the dorsal and ventral side, by 1−6 in dorsal and by 3−7 in ventral bundles; bifid chaetae are generally prevailing in anterior, and simple ones in posterior bundles, ventral chaetae bundles with large glands; X ventral chaetae unmodified; XI at each male pore a genital spermathecal type chaeta, slightly sigmoid, with narrow, grooved, acute distal portion shorter than the proximal shaft, embedded in large setal gland and equipped with a large, prostata-like accessory gland; L = 2.7−3.8 mm; caves ..... *Rhyacodriloides aeternorum* Martin, Martínez-Ansemil & Sambugar, 2010
[Italy]

Oligochaeta: Tubificida: Tubificidae: *Psammoryctides*: Species

1 Single thin, stick-formed, grooved spermathecal chaetae in X of sexually mature individuals 2

1′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals 7

2(1) No penis sheaths 3

2′ Penis sheaths present, short tubular, with narrow middle portion and slightly wider proximal end, widest distally, its edges transitioning into the penis sac inner fold; dorsal hair chaetae anteriorly 1−2 per bundle, in midbody single, in hindbody none; anteriorly 4−7, posteriorly 2−5 pectinates, in anterior bundles with equal main teeth and with three intermediate denticles, backwards with longer upper tooth and two intermediate denticles; ventral bifids anteriorly 4−8 per bundle and with upper tooth length two times lower; posteriorly 2−5, tooth length difference decreasing; no ventral chaetae in XI(?); L = 13−14.5 mm; caves (Fig. 12.12(47−51)) ..... "*Psammoryctes*" *hadzii* Karaman, 1974, incertae sedis
[Slovenia]

3(2) Pectinate chaetae not spatulate 4

3′ Anterior dorsal bundles with 1−4 smooth or very finely pilose hair chaetae and 3−8 spatulate pectinate chaetae; numerous intermediate denticles of the latter fusing with the long main teeth to form broad, longitudinally folded blade; anterioventral chaetae 3−4, with upper tooth longer; hair chaetae gradually disappearing in posterior segments while only 2−3 thick, strongly curved crotchets remain in the dorsal and ventral bundles; L = 30−70 mm (Fig. 12.12(24−29)) ..... *Psammoryctides barbatus* (Grube, 1861)
[western Palaearctic]

4(3) No prolonged hair chaetae in midbody 5

4′ Hair chaetae 1−2 in forebody and gradually disappearing posteriorly, finely pilose, very long, to 1.6 mm in midbody; dorsal pectinate chaetae 1−3 per bundle, the smallest in II−III, with 2−5 short intermediate denticles, replaced with robust bifid crotchets in the posterior half of body; ventral crotchets 1−3 in anterior and 1−2 in posterior segments, with thinner upper tooth; in II−III they are smallest, with teeth equally long while chaetae robustness increases and upper tooth size decreases posteriorly; L = 17−22 mm (Fig. 12.12(30−37)) ..... *Psammoryctides longicapillatus* Martínez-Ansemil & Giani, 1983
[Lebanon, Turkey]

5(4) Hair chaetae thin and flexible, finely pilose 6

5′ Hair chaetae relatively thick, stiff and roughly pilose, 1−3 in anterior and single in posterior bundles; anterior pectinate chaetae 2−3 per bundle, curved and with shorter upper tooth, with thick, short intermediate denticles; II−III anterior most ventral crotchets 1−3 per bundle, with subequal teeth; upper tooth becoming gradually shorter and thinner posteriorly; posterior crotchets, both dorsal and ventral, very thick, their big lower tooth bent at almost 180° to chaetal axis; L = 70−100 mm (Fig. 12.12(38−44)) ..... *Psammoryctides albicola* (Michaelsen, 1901)
[western Palaearctic]

6(5) Short hair chaetae in forebody only, or lacking; forebody pectinate chaetae with equal teeth or slightly longer upper tooth, and with 1−5 short intermediate denticles; ventral chaetae 3−4 per bundle, with longer upper tooth; mid- and hindbody both dorsal and ventral bundles with single robust, strongly curved bifid chaetae; in some individuals (f. *variabilis*) the ventral and dorsal chaetae may be similar, bifid only; L = 30−42 mm ..... *Psammoryctides ochridanus* (Hrabě, 1931)
[Albania/Macedonia/Greece: Lakes Ohrid and Prespa]

6′ Hair chaetae anteriorly 1−5 per bundle, disappearing in midbody; pectinate chaetae 2−3 in anterior bundles, with equal teeth and numerous, twice as short intermediate denticles; anterior ventral chaetae 2−4, with longer upper tooth; posterior crotchets, both dorsal and ventral, thick and curved; L = 20−30 mm (Fig. 12.12(45, 46)) ..... *Psammoryctides moravicus* (Hrabě, 1934)
[Europe; Near East]

7(1) Midbody and tail region with scarce, thick, strongly curved bifids in all bundles, with thick lower and much shorter and thinner upper tooth; ventral chaetae lacking in XI and XI 8

7′ Ventral bifid chaetae thick along the whole body, present in XI but lacking in IX(?) and X, in anterior bundles 2−3 (4), sigmoid and with equally long teeth but upper tooth shorter; posterior region only 1−2 bifids both in dorsal and ventral bundles, larger than in forebody, upper tooth becoming gradually smaller and angle between teeth larger; dorsal hair chaetae 1−2 in fore- and midbody, pilose; in forebody dorsal pectinate chaetae 1−4, sigmoid, thick, with equally thick, short teeth, and 2−5 much shorter intermediate teeth; posterior chaetae described as bearing long bunches of 4−30 thin pilose threads attached between teeth (maybe bacterial?); L = 16−21 mm ..... *Psammoryctides stankoi* (Karaman, 1974)
[Kosovo: Šar Mountains]

8(7) Hair chaetae and pectinate or palmate chaetae present in anteclitellar dorsal bundles 9

8′ No hair or pectinate chaetae; bifids two to four in anteclitellar and 1−2 in posterior segments, with shorter upper tooth, in posterior segments with lower tooth much thicker and curved; L = 9−13 mm; brackish water ..... *Psammoryctides deserticola lastockini* (Jarošenko, 1948)
[Black Sea estuaries; Caspian Sea]

9(8) Anterior dorsal bundles with 1−3 pectinate chaetae, the latter with equally long or slightly longer upper tooth, and usually with several short intermediate denticles, plus 1−2 pilose hair chaetae; anterior ventral bundles with 2−3 bifids, the upper tooth equally long or slightly longer but always thinner; caudally both dorsal and ventral bundles with a single thick, curved bifid chaeta with very thick, curved lower tooth, the upper small and erect; L = 25−30 mm; fresh- and brackish water (Fig. 12.16(8−11)) ..... *Psammoryctides deserticola deserticola* (Grimm, 1876)
[Ponto-Caspian Basin, Danube River, Balkan Peninsula, Near East]

9′ Anteclitellar dorsal bundles with 5−10 palmate chaetae with numerous intermediate denticles subequal to main teeth, plus 3−6 hair chaetae; anteclitellar ventral bundles of 3−5 bifids with stout teeth, the upper one slightly shorter; all postclitellar bundles with only bifids, the upper tooth becoming still shorter, the lower one more curved; their number decreasing to one in dorsal and two in ventral bundles caudally; L = 9−15 mm; springs ..... *Psammoryctides hrabei* (Karaman, 1971)
[Macedonia: Demir Kapija]

Oligochaeta: Tubificida: Tubificidae: *Potamothrix*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent 17

2(1) Modified genital chaetae present in sexually mature individuals 3

2′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals 16

3(2) Bifid (and pectinate, when present) chaetae with subequal teeth or upper tooth longer 4

3′ Anterior dorsal bundles with 2−5 short, curved hair chaetae and 4−6 bifid chaetae with somewhat shorter and thinner, slightly rounded upper tooth; anterior ventral chaetae 3−10 per bundle, with shorter upper tooth; similar hair and bifid chaetae but fewer posteriorly; spermathecal chaetae in X straight and thick, with relatively broad groove; L = 15−21 mm (Fig. 12.13(12−14)) ..... *Potamothrix vejdovskyi* (Hrabě, 1941)
[Ponto-Caspian; invasive in Europe and Nearctic]

4(3) No extra long hair chaetae 5

4′ Dorsal bundles with 1−2 smooth hair and one to three (4) pectinate (forebody only; with 1−4 fine intermediate denticles) or bifid chaetae; forebody hair chaetae very long, to 1.2 mm; forebody ventral chaetae 2−5, hindbody 3−4 per bundle, with slightly longer upper tooth; X spermathecal chaetae one or two, longer and thicker than bifids, straight, with relatively broad groove; L = 15−20 mm; thermal streams ..... *Potamothrix thermalis* (Pop, 1967)
[Romania]

5(4) Hair chaetae present in preclitellar segments 6

5′ Hair chaetae only in midbody, 1−2 per bundle, not much longer than bifid chaetae; bifids 5−10 in forebody and 3−4 in hindbody, similar in dorsal and ventral bundles, with equally long teeth but upper tooth thinner; spermathecal chaetae with relatively broad groove, equipped with 1−2 separate glands; L = 25−33 mm ..... *Potamothrix prespaensis* (Hrabě, 1931)
[Albania/Macedonia/Greece: Lakes Ohrid and Prespa]

6(5) Grooved genital chaetae at spermathecal pores only, with more or less symmetrical distal portion 7

6(5) Uniform genital chaetae asymmetrically scalpel- or beak-shaped, with groove on convex edge, present in up to three pairs at spermathecal and male pores in VII−IX or IX−XI; vegetative reproduction by architomy (fragmenting) prevailing; in mature individuals reproductive system mostly shifted forward two segments, with male pores in IX and two pairs of spermathecae in VII and VIII; anterior dorsal bundles with 3−5 hair and 3−4 pectinate chaetae, the latter with slightly longer upper tooth and with fine intermediate denticles; anterior ventral chaetae 2−5, with longer upper tooth; L = 10−18 mm (Fig. 12.12(1−5)) ..... *Potamothrix bedoti* (Piguet, 1913)
[Holarctic]

7(6) Main part of spermathecal chaetae straight. Hair chaetae beginning in II 8

7′ Spermathecal chaetae (in most species) either slightly sigmoid or curved in one direction; hair chaetae begin in III or further back (at II in one species); ancient lakes in Yunnan, SW China 12

8(7) Spermathecal chaetae with narrower distal portion, not cordate 9

8′ Spermathecal chaetae in X cordate or spear-shaped, with distal portion very broad and flat; anterior dorsal bundles 1−5 hair chaetae and 2−5 pectinate chaetae with short intermediate denticles; anterior ventral bundles 2−4 bifid equal chaetae; chaetal number decreasing posteriorly; L = 15−35 mm; in slightly brackish and fresh water (Fig. 12.13(7)) ..... *Potamothrix bavaricus* (Oschmann, 1913)
[cosmopolitan]

9(8) Spermathecal chaetae thicker than ventral bifid chaetae; the margins of the narrow spatulate distal portion may be slightly convex and their proximal end curved 10

9′ Spermathecal chaetae long and thin, the grooved distal portion with parallel edges, the distal end with sharp hooked tip; proximal end hooked; anterior dorsal bundles 2−5 hair chaetae and 2−5 thin pectinates with short intermediate denticles; anterior ventral bundles with 3−5 bifid chaetae with slightly longer and thinner upper tooth; teeth equally long in posterior chaetae; L = 6−15 mm (Fig. 12.13(8)) ..... *Potamothrix heuscheri* (Bretscher, 1900)
[western Palaearctic. Introduced(?) North Africa and Neotropics]

10(9) Clitellum without ventrolateral body wall outgrowths 11

10′ Clitellum in X/XI body wall with short ventrolateral alate outgrowths; anterior dorsal bundles with 1−3 hair and 1−4 pectinate chaetae with several intermediate denticles; posterior dorsal bundles with one hair and one bifid chaeta; anterior ventral bundles 2−3 chaetae with teeth of equal length but upper tooth thinner than lower; posteriorly ventral chaetae 2−3, upper tooth becoming slightly shorter; X spermathecal chaetae sitting in a large gland, straight; L = 15−17 mm; brackish water ..... *Potamothrix alatus alatus* Finogenova, 1972
[Caspian Sea; Ukraine: Dnepr−Bug Estuary]

..... (Fig. 12.13(15−19)) *Potamothrix alatus hazaricus* Timm & Arslan, 2013
[Turkey: Lake Hazar]

11(10) Spermathecal chaetae in X with narrow, cupped, grooved distal portion with slightly convex, undistorted edges; anterior dorsal bundles with 1−4 hair and 4−6 pectinate chaetae with 3−4 intermediate denticles; posterior dorsal bundles with one hair and one bifid chaeta; anterior ventral bundles 2−10(12) bifid chaetae with upper tooth 1.5−2 times longer than lower; posteriorly ventral chaetae 1−2, upper tooth slightly longer than lower; L = 7−55 mm (the largest at greater depths) ..... *Potamothrix alatus paravanicus* Poddubnaja and Pataridze 1989
[Armenia; Georgia]

11′ Spermathecal chaetae in X with narrow, cupped, often slightly distorted, grooved distal portion; anterior dorsal bundles with 1−5 hair chaetae and 3−5 pectinates with upper tooth slightly longer than lower, with several slightly shorter intermediate denticles (a form without hair chaetae in fully mature individuals, f. *lacustris* Lastočkin, 1927 is described from a Russian lake); anterior ventral chaetae three to six, bifid with upper tooth slightly longer and thinner; chaetal number decreasing posteriorly, with teeth becoming equally long; L = 15−45 mm (Fig. 12.13(1−6)) ..... *Potamothrix hammoniensis* (Michaelsen, 1901)
[western Palaearctic. Introduced elsewhere]

12(7) Penial sheath absent; ventral chaetae absent at male pores in XI 13

12′ Penes in XI with short, distally oblique sheath; II–V dorsal bundles consisting of 6–9, anterior ventral bundles of 6–9, and posterior ventral bundles 2–4 (5) bifid chaetae, with upper tooth somewhat thicker and twice as long as lower tooth, which is usually bluntly bifurcate; hair chaetae from VI, 3–8 per bundle, pilose, accompanied by 3–7 pectinates with bifurcate lower tooth and 1–2 intermediate denticles; some pectinates with upper tooth slightly bifurcated; spermathecal chaetae in XI short and thin, arched, grooved distal portion bifurcate; at male pores in XI 2–3 bifid chaetae with lower tooth shorter than upper but not bifurcated; L ≥ 7.2 mm (Fig. 12.13(9–11)) ..... *Potamothrix scleropenis* Cui & Wang, 2005
[China: Lake Fuxian]

13(12) Reproductive system not shifted anteriorly 14

13′ Reproductive system shifted anteriorly, with spermathecal pores in VIII and male pores in X; II (or II–IV) dorsal bundles consist of 7–8, anterior ventral bundles of 6–10, and posterior ventral bundles 3–5 bifid chaetae, with upper tooth longer and thicker than lower tooth; hair chaetae from III(V), anteriorly 4–8 and posteriorly by 2–4 per bundle, pilose; accompanied in forebody by 5–8 and in hindbody by 3–4 pectinate chaetae with usually slightly longer upper tooth, bifurcate lower tooth, and 1–3 intermediate denticles; spermathecal chaetae in VIII, arched, with strongly curved proximal end embedded in glandular sac; L = 8.9–19.8 mm ..... *Potamothrix parabedoti* Cui & Wang, 2012
[China: Lake Fuxian]

14(13) Hair chaetae beginning either in II or VII; spermathecal chaetae not sigmoid 15

14′ II–IV dorsal bundles consisting of 7–10, anterior ventral bundles of 6–8, and posterior ventral bundles 2–4 (5) bifid chaetae, with upper tooth longer and thinner than lower tooth, the latter occasionally bifurcate; hair chaetae beginning from V, anteriorly 5–8 per bundle, pilose, accompanied in forebody by 5–7 pectinate chaetae with upper tooth slightly longer or as long as the bifurcate lower tooth, and with 1–2 intermediate denticles; posterior dorsal bundles with 1–4 hair chaetae and 2–6 bifid chaetae; X spermathecal chaetae slightly sigmoid, in glandular sacs; L = 7.6 mm ..... *Potamothrix praeprostatus* Cui & Wang, 2012
[China: Lake Fuxian]

15(14) II–VI dorsal bundles with only bifid chaetae 7–8, with slightly longer and thicker upper tooth; from VII, 1–6 pilose hair chaetae and 3–6 similar bifid or pectinate chaetae with 1–2 intermediate denticles; ventral chaetae 6–8 per bundle anteriorly and 2–4 (5) in postclitellar segments, similar to the anterior dorsal chaetae; spermathecal chaetae almost straight, with grooved and contorted distal portion; both vas deferens and spermathecal duct reduced; L = 9.2–11.8 mm ..... *Potamothrix aductus* Cui & Wang, 2012
[China: Lake Fuxian]

15′ Hair chaetae in dorsal bundles beginning from II, smooth (0) 1–4 per bundle besides bifid or (mostly) pectinate chaetae with slightly longer and thinner upper tooth and 2–3 fine intermediate denticles; ventral chaetae anteriorly 3–7, with conspicuously longer and thinner upper tooth; spermathecal chaetae distally grooved, curved proximally; penis scabrous; L = 4.0–8.7 mm ... *Potamothrix rhytipeniatus* Cui & Wang, 2012
[China: Lake Xingyun]

16(2) Dorsal hair chaetae present only in postclitellar segments, short, 1–2 per bundle; no pectinates; preclitellar bundles only bifid chaetae, 4–7 per bundle, with shorter and thinner upper tooth; similar chaetae, 5–8 per bundle in midbody and 2–3 in posterior region; XI ventral bifids 1–4; "hearts" in VIII; L = 20–25 mm ..... *Potamothrix ochridanus* (Hrabě, 1931)
[Albania/Macedonia: Lake Ohrid]

16′ Dorsal hair chaetae 1–2 per bundle, present along whole body; fore- and midbody 3–5 pectinate chaetae with equal teeth and 3–4 intermediate denticles; hindbody with 2–3 bifid chaetae with equal teeth; anteriorly ventral bifid chaetae 3–5, rearward 3–4, all with longer upper tooth like dorsal bifids; L = 9.6–10.7 mm; groundwater .... *Potamothrix postojnae* Karaman, 1974
[Slovenia]

17(1) Chaetae at least in anterior bundles with equal teeth or upper tooth longer (although often thinner) 18

17′ Most chaetae, at least in anterior bundles, with shorter and thinner upper tooth; male pores may lie in X, XI, XII, XIII, or XV, with spermathecal pores in previous segment; anterior chaetae 3–7 per bundle, only 1–2 ventrally in genital segments, posteriorly 2–4; chaetal teeth equal or upper tooth slightly thinner; dissepiments 3/4–10/11 (when male pores in XII) thickened; L = ∼20–25 mm; fresh- and brackish water ..... *Potamothrix mrazeki* (Hrabě, 1941)
[Black Sea; Caspian Sea; Danube River]

18(17) Modified genital chaetae present in X or also in XI 19

18′ No modified genital chaetae in X 25

19(18) Grooved spermathecal chaetae in X, single bifid penial chaetae with longer upper tooth in XI 20

19′ No modified penial chaetae in XI 22

20(19) Spermathecal chaetae slender, with grooved portion shorter that shaft 21

20′ Spermathecal chaetae in X short and thick, their shaft shorter than grooved part, slightly contorted distally with curved tip; single bifid penial chaetae at male pores in XI, with distal tooth thinner and straighter; anterior bundles ordinary chaetae 5–9, with equal length teeth, upper tooth thinner; chaetal number decreasing posteriorly; conical penes; L = 15–40 mm; freshwater (Fig. 12.18(17–20)) .... *Potamothrix moldaviensis moldaviensis* Vejdovský & Mrázek, 1903
[western Palaearctic. Invasive in Nearctic]

21(20) Spermathecal chaetae with grooved portion slightly shorter than shaft; penial chaetae with upper tooth twice longer; ordinary chaetae 4−8, in anteriormost segments with shorter but posteriorly with slightly longer upper tooth; spermathecal pores ventral; L = 8−15 mm; brackish water ..... *Potamothrix moldaviensis mitropolskiji* (Hrabě, 1950)
[Caspian Sea]

21′ Spermathecal chaetae with grooved part more than twice as short as shaft, sitting in glandular pouch and equipped with large accessory gland; penial chaetae relatively thin, with twice longer upper tooth; ordinary chaetae in forebody 4−10, with teeth of subequal length but the upper tooth thinner; spermathecal pores lateral; L = 10−15 mm; brackish water ..... *Potamothrix grimmi* (Hrabě, 1950)
[Caspian Sea]

22(19) Spermathecal chaetae straight 23

22′ Spermathecal chaetae in glandular sacs, thin, curved, with grooved distal portion; forebody chaetae 4−6 dorsally and 3−6 ventrally, with longer and thinner upper tooth; 1−2 small bifid chaetae at male pores in XI, with equal teeth; no penes (Fig. 12.18(28−30)) ..... *Potamothrix paramoldaviensis* Cui & Wang, 2012
[China: Lake Fuxian]

23(22) Ordinary chaetae with teeth of equal length 24

23′ Ordinary chaetae in forebody three to eight, in hindbody 3−6, in XI ventrally 1−2, teeth more or less equal but in forebody beginning from III the upper tooth slightly longer; spermathecal pores dorsolateral; spermatozeugmata vermiform; L = 4−7 mm; brackish water ..... *Potamothrix manus* Finogenova, 1976
[Caspian Sea]

24(23) Chaetae 3−7 per bundle, teeth equal length, upper tooth thinner; dissepiments 3/4−9/10 thickened; L= 15−30 mm ..... *Potamothrix danubialis* (Hrabě, 1941)
[Black Sea estuaries; Danube River]

24′ Forebody chaetae 7−10 per bundle, posteriorly three, teeth equal length, upper tooth thinner; no thickened dissepiments; L = ∼25 mm ..... *Potamothrix isochaetus* (Hrabě, 1931)
[Albania/Macedonia: Lake Ohrid]

25(18) No modified genital chaetae; bifids in forebody 5−8 and with slightly longer upper tooth, in hindbody 3−4 and with teeth becoming equal; ventrally in X five, and in XI two bifids; no thickened dissepiments; spermathecal poes lateral, spermatozeugmata vermiform; L = 7.5 mm ..... *Potamothrix cekanovskajae* Finogenova, 1972
[Caspian Sea]

25′ Blunt penial chaetae or penis sheaths in XI present or lacking(?); dissepiments 3/4−10/11 thickened; chaetae 3−6 per bundle but only 2−3 ventrally in X and 1−2 in XI; upper tooth longer and thinner than lower, the longest (two times) in midbody; teeth tips often rounded; spermatozeugmata with one end expanded and the most part caudiform; L = 20−30 mm; brackish water ..... *Potamothrix caspicus* (Lastočkin, 1937)
[Black Sea estuaries; Caspian Sea]

Oligochaeta: Tubificida: Tubificidae: *Isochaetides*: Species (excluding Lake Baikal)

1 Hair chaetae absent 2

1′ Hair chaetae present; modified genital chaetae present in sexually mature individuals; penis sheaths thin, slightly conical, not covering the penis distal end; proximal ends fungiform, gradually transitioning into cuticular lining of penial sac inner fold; hair chaetae 1−3 per bundle in anterior and 1−2 posteriorly, becoming gradually shorter; pectinates 2−4 in anterior dorsal bundles, with acute main teeth and 1−2 shorter intermediate teeth; posterior dorsal chaetae by 2−3, bifid with thinner and shorter upper tooth; ventral chaetae 4−6 in anterior bundles, with subequal teeth, reduced to two in tail region, upper teeth becoming thinner and shorter; bifid chaetae 1−2 also ventrally in XI; X modified spermathecal chaetae single, with acute, grooved distal part and strongly curved proximal part; bifid chaetae 1−2 ventrally in XI; L = 8−10 mm; karstic springs ..... *Isochaetides gianii* Rodriguez & Achurra, 2010
[Spain]

2(1) No palmate chaetae; penis sheaths present or absent 3

2′ All dorsal chaetae palmate with 5−8 intermediate denticles as long as main teeth, 6−15 in anterior bundles and 2−6 (8) posteriorly; ventral chaetae mostly pectinate, with longer upper tooth and with 1−3 short intermediate denticles, 5−10 per bundle anteriorly and 2−5 posteriorly; XI male pores without ventral chaetae; penis sheaths absent; L = 7−20 mm ..... *Isochaetides palmatus* He, Cui & Wang, 2012
[China: Lake Yamzho Yumco in Tibet]

3(2) Chaetae at least in anterior bundles with equal teeth or upper tooth longer (although often thinner) 4

3′ Most chaetae, at least in anterior bundles, with shorter and thinner upper tooth; single modified genital chaetae in ventral bundles of IX, X, and XII, with upper tooth length ≥ twice lower, lower laterally dilated; XI male pores without ventral chaetae; ordinary chaetae in anterior bundles 3−7, with shorter upper tooth, sometimes both teeth worn; posteriorly chaetal number and difference in teeth length decreasing; L = 25−33 mm (Fig. 12.17(24−31)) ..... *Isochaetides michaelseni* (Lastočkin, 1936)
[western Palaearctic]

4(3) Grooved spermathecal chaetae present in X or also in some neighboring segments 5

4′ X ventral chaetae bifid or lacking, not modified; blunt penial chaetae or penis sheaths present or lacking; anterior chaetae 6–8 (11) per bundle, teeth blunt, upper one slightly longer; posteriorly chaetae three, mostly with shorter upper tooth; small penis in very long sac, without sheath; spermatozeugmata scarce (one to two), pyriform; L = 20–42 ..... *Isochaetides tomilovi* Semernoy & Akinshina, 1980 [Mongolia: Lake Hubsugul]

5(4) Length of teeth can vary in a chaetal bundle, from upper tooth slightly longer to shorter than lower; thin spermathecal chaetae with grooved distal portion and curved proximal end, in a glandular sac 6

5′ Anterior bundles chaetae 3–5, with longer upper tooth; in tail region two; X with single spermathecal chaetae with narrow, grooved distal portion and sharp tip; penis sheaths thin-walled, cylindrical or bent, length 2.7 times width; esophagus chloragogen tissue beginning either in V or VI; dissepiment 3/4 thicker than the subsequent ones; VIII–X with three pairs of "hearts"; L = 8–13 mm; brackish water lakes (Fig. 12.18(40–43)) ..... *Isochaetides suspectus* (Sokolskaja, 1964) [Russia: Sakhalin Island]

6(5) Penis fusiform or irregularly cylindrical; atrial duct short; chaetae 4–9 per bundle in forebody and 3–4 posteriorly; L= 25–38 mm .... *Isochaetides baicalensis* (Michaelsen, 1901) [Russia: Lake Baikal and Angara River]

6′ Penis elongate conical; atrial duct long; chaetae 5–9 per bundle; "hearts" in VIII and IX; L = 15–35 mm (Fig. 12.20(35–38)) .... *Isochaetides arenarius* (Michaelsen, 1926) [Russia: Lake Baikal and Angara River]

Oligochaeta: Tubificida: Tubificidae: *Varichaetadrilus*: Species

1 Ventral chaetae at genital pores unmodified or lacking even in mature individuals 2

1′ Modified genital chaetae present in sexually mature individuals; penis sheaths thin, short cylindrical; anteriormost dorsal bundles only bifid chaetae with upper tooth thicker and twice as long as lower, 3–8 per bundle; subsequent preclitellar dorsal bundles (from IV–VIII to IX–X) 3–5 smooth hair chaetae and 5–8 bifids with equal teeth or upper one slightly longer; dorsal bundles of genital segments only bifids; posteriorly 2–5 hair and 3–6 bifid chaetae, sometimes also simple chaetae; no pectinates; ventral bifid chaetae similar, in anterior bundles 6–8, posteriorly 3–5, IX lacking; spermathecal chaetae in X or IX singular, curved, distally acute and grooved, proximal part embedded in a glandular sac; 1–2 smaller bifids at male pores in X or X; L = 11–30 mm .... *Varichaetadrilus vestibulatus* Cui & Wang, 2009 [China: Lake Fuxian]

2(1) Penis sheaths at least as long as wide; ventral chaetae without intermediate denticles 3

2′ Penis sheaths thin-walled and very short, surrounding only penis distal portion; dorsal anterior bundles pilose (serrate?) hair chaeta and two pectinates with upper tooth longer than lower, with a few intermediate denticles; no hair chaetae posteriorly; ventral bifids (pectinates) 2–3 anteriorly, upper tooth longer than lower, and a single intermediate denticle; no modified genital chaetae (presence of bifids at male pores in XI?); L = ~7 mm; freshwater, inland brackish water ..... *Varichaetadrilus israelis* (Brinkhurst, 1971) [Israel]

3(2) Penis sheaths subglobular, not much longer than wide; anterior dorsal bundles 4–6 smooth hair chaetae and 4–6 pectinates with equal teeth, upper tooth thinner, 1–2 thin intermediate denticles; posteriorly intermediate denticles vanishing while tooth shape does not change; ventral chaetae 5–6 in anterior and by 2–3 in posterior segments, upper tooth slightly longer and thinner; genital segments ventral chaetae not modified; L = 11–16 mm (Fig. 12.15(7–11)) ..... *Varichaetadrilus potatiensis* (Sokolskaja, 1983) [northeastern Russia: Lake Potatgythyn in Koryak Mountains]

3′ Penis sheaths length ~two times expanded proximal portion width; distal end wider than middle; midbody and tail region two thick and strongly curved bifids in all bundles, with very thick lower, and much shorter and thinner upper tooth; dorsal bundles with a thin hair chaeta; anterior dorsal bundles with 1–2 very thin and smooth hair chaetae and with 2–3 slender pectinates with several short intermediate denticles; anterior ventral bifids 3–4 per bundle, with teeth equally long, upper tooth thinner; XI ventral bundles two ordinary bifids; dilated lateral blood vessels ("hearts") in IX; sexually mature individuals, clitellar region ventral side concave, framed by lateral folds of body wall; reproducing mainly by fragmentation, seldom maturing; L = 26–29 mm when mature (Fig. 12.15(1–6)) .... *Varichaetadrilus harmani* (Loden, 1979) [Nearctic. Introduced in Europe]

Oligochaeta: Tubificida: Tubificidae: *Rhyacodrilus*: Species (excluding Lake Baikal)

1 Hair chaetae present 2

1′ Hair chaetae absent 20

2(1) Modified genital chaetae present in sexually mature individuals 3

2′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals; anterior dorsal bundles one hair chaeta (seldom two) and 2–3 bifids with upper tooth shorter and thinner; posterior dorsal bundles with 3–4 simple-pointed crotchets; ventral chaetae with much shorter upper tooth, 4–5 per bundle in anterior bundles and 3–4 posteriorly; L = 6.5 mm; groundwater (Fig. 12.16(32–34)) .... *Rhyacodrilus lindbergi* Hrabě, 1963 [western Europe]

3(2) Single modified, bifid (but not grooved) spermathecal chaetae with long upper tooth present at least in X, blunt penial chaetae at male pores in XI 4

3′ Modified genital chaetae present at male pores only (sometimes hidden in body wall) 7

4(3) Modified, bifid spermathecal chaetae only in X 5

4′ Bifid "spermathecal" chaetae in IX, X, and XII, 1−2 per bundle, with lower tooth dilated, upper tooth three times longer and thin; XI at male pores penial chaetae 5−6 per bundle, with simple blunt tip; anterior dorsal bundles 2−3 hair and 2−3 pectinate chaetae with lyrifrom apex and 5−7 intermediate denticles; postclitellar pectinates with teeth curved in one direction; caudally only bifids in dorsal bundles, with very long and thin lower tooth diverging at obtuse angle; anterior ventral locomotory chaetae to seven per bundle, bifid with considerably longer upper tooth; posteriorly the number decreases gradually to 1−2 while the upper tooth becomes shorter; L = 10−12 mm (Fig. 12.13(27−33)) ..... *Rhyacodrilus tauricus* Dembitsky, 1975 [Ukraine: Crimea]

5(4) Dorsal bifid or pectinate chaetae with upper tooth not considerably longer than lower 6

5′ Dorsal pectinate chaetae with much longer and thinner upper tooth and several shorter intermediate denticles, 3−4 in anterior bundles, and 2−3 with equally long teeth in tail region; anterior dorsal bundles with two pilose hair chaetae; anterior ventral bundles with 4−6 (7) bifid chaetae, the upper tooth being considerably longer and slightly thinner; postclitellar segments 2−3 ventral chaetae per bundle, and difference in tooth length decreases; X with 2−3 spermathecal chaetae per bundle, larger than locomotory chaetae, with very long upper and short lower tooth; XI penial chaetae 3−4, almost straight, with bent, usually short, bifid tip; L = 9−14 mm (Fig. 12.13(39−44)) ..... *Rhyacodrilus svetlovi* Sokolskaja, 1976 [Russia: Chukchi Peninsula]

6(5) Anterior dorsal bundles 1−2 hair and 1−2 bifid or pectinate chaetae (the latter with obscure intermediate denticles) with subequal teeth; upper tooth becomes thinner and shorter in posterior bundles; anterior segment ventral chaetae (3) 4−5, with upper tooth 1.3−1.5 times longer than proximal; posteriorly, upper tooth becomes gradually slightly shorter; X spermathecal chaetae with widely diverging teeth, upper tooth length 2.5 times proximal, the chaeta curved proximal portion sitting in glandular sac; XI penial chaetae (1?) 2, straight but with slightly curved blunt (simple or bifid?) tip; L ≥ 4 mm; groundwater ..... *Rhyacodrilus gasparoi* Martínez-Ansemil, Sambugar & Giani, 1997 [Italy]

6′ Dorsal bundles with 1−2 smooth hair chaetae in fore- and midbody, and (1)2(3) crotchets along the whole body; crochets pectinate, with equal teeth in anterior segments, with upper tooth progressively reduced in middle region; posterior dorsal chaetae simple and strongly curved; anterior ventral bundles with (3) 4−5 bifids, upper tooth length 1.8−2.3 times lower; posteriorly the upper tooth becomes progressively shorter and chaetae distal portion more curved; X spermathecal chaetae, slightly sigmoid and bifid, with upper tooth length 3.5 times proximal; XI penial chaetae 1−2, almost straight but distally curved, with simple blunt tip; a large mass of finely granulated cells at penial chaetae; atria without any prostate cover; small species; groundwater ..... *Rhyacodrilus glandulosus* (Martínez-Ansemil, Sambugar & Giani, 1997) [Slovenia]

7(3) Penial chaetae in XI single or by 1−2 8

7′ Penial chaetae more than 1−2 per bundle 12

8(7) Posterior bifid chaetae becoming gradually single-pointed or with reduced upper tooth 9

8′ Posterior segments upper tooth not reduced (sometimes shorter than lower one) 10

9(8) Anterior dorsal bundles with 1−2 hair chaetae and 1−3 pectinates with upper tooth thinner and slightly shorter, and with few intermediate denticles; posterior dorsal bundles with 1−4 sigmoid crotchets, with rudimentary upper tooth or with simple sharp tip; anterior ventral bundles 2−6 bifids with upper tooth length 1.5−2.5 times lower; posterior segments 1−4 bifids with equal teeth, but upper one thinner; at male pores penial chaetae 1−2, with curved tip and strongly reduced or missing upper tooth; reproductive system position variable, with male pores in X, XI, or XII, maybe in connection with asexual reproduction by architomy; L = 3−6 mm; groundwater (Fig. 12.14(1−6)) ..... *Rhyacodrilus amphigenus* Juget, 1987 [France]

9′ Anterior dorsal bundles with 1−2 finely pilose hair chaetae and (1) two (3) bifid or pectinate crotchets (the latter with hardly visible intermediate denticles) with teeth subequal; hair chaetae gradually disappear posteriorly while crotchet number increases to (2) 3−5 (6), the upper tooth reducing and finally disappearing in last segments; ventral chaetae in foremost segments (4) 5−6 (7), in VIII−X 1−4, in postclitellar segments 3−5 (6); in anteclitellar chaetae upper tooth thicker, 2−3 times longer than proximal while the upper tooth becomes shorter posteriorly and may disappear; XI penial chaetae single, simple-pointed, with distal portion thin and curved; body spotted with brownish granular secretion, mainly in middle and posterior regions; L = 3.8−4.3 mm mm; groundwater ..... *Rhyacodrilus omodeoi* Martínez-Ansemil, Sambugar & Giani, 1997 [Slovenia]

10(8) Pectinate chaetae teeth not widely diverging 11

10′ Anterior dorsal bundles one (2) hair and 1−2 pectinate chaetae with teeth widely diverging, intermediate denticles very fine; postclitellar dorsal bundles with 1−2 bifids with upper tooth thinner and shorter; ventral bundles 3−4 bifids, upper tooth 2−3 times longer in preclitellar segments but becoming shorter than lower posteriorly; penial chaetae in XI single, almost straight, with blunt tip; L ≥ 4 mm; groundwater ..... *Rhyacodrilus dolcei* Martínez-Ansemil, Sambugar & Giani, 1997 [Italy]

11(10) Anterior dorsal bundles with 1−3 smooth hair chaetae and 2−3 (5) pectinates with upper tooth straighter and twice longer than the lower, with numerous very thin intermediate denticles; anterior ventral bundles 2−6 crotchets with upper tooth twice longer; posteriorly 1−4 bifid crotchets, with teeth becoming subequal or upper tooth slightly shorter; XI male pores penial chaetae single, with simple obtuse strongly curved tip; L = 6−17 mm; streams and groundwater (Fig. 12.14(7−10)) ..... *Rhyacodrilus subterraneus* Hrabě, 1963 [Europe. Nearctic]

11′ Dorsal bundles 1−3 hair chaetae and 1−2 pectinates with equal teeth and 2−3 intermediate denticles in anterior, and 1−2 bifids with upper tooth shorter in posteriorly; ventral bifid chaetae 3−6 in anterior and 3−4 in posterior bundles, anteriorly with much longer and thicker upper tooth; midbody teeth become gradually equal, tail region upper tooth shorter and thinner; XI penial chaetae single, slightly longer than locomotory chaetae, relatively thick, with distal nodulus and asymmetrically sharp tip; L = 3.0−4.1 mm; groundwater ..... "*Rhyacodrilus*" *sketi* Karaman, 1974, incertae sedis [Slovenia]

12(7) Penial chaetae with blunt tip or with reduced upper tooth 13

12′ XI penial chaetae 2−3 per bundle, thin and stick-formed, gradually tapering to a sharp arched ectal end; anterior dorsal bundles with 2−3 smooth hair chaetae and 2−3 (4) pectinate chaetae with equal, long parallel teeth and shorter intermediate denticles; upper tooth and intermediate denticles diminish and disappear gradually posteriorly, until only one hair chaeta, one bifid chaeta, and one simple-pointed chaeta remain in the last dorsal bundles; anterior ventral bundles up to six bifid chaetae with somewhat longer upper tooth; posterior upper tooth becomes gradually as long as lower or shorter; L = ∼10 mm; lakes (Fig. 12.14(16−20)) ..... *Rhyacodrilus altaianus* Michaelsen, 1935 [Russia: Altai Mountains in Siberia]

13(12) Body wall monochrome, not spotted 14

13′ Body spotted with brown epidermal glands secretion; anterior dorsal bundles 2−5 long and one short hair chaeta; midbody single short hair chaeta, absent in posterior region; forebody dorsal pectinate chaetae 3−6 (8), midbody 4−5, hindbody 2−4, with slightly thinner upper tooth and 6−10 shorter intermediate denticles; posterior pectinates lower tooth becomes thicker and more curved while intermediate denticles dwindle; ventral chaetae 3−5 per bundle, the number decreasing to two in the tail region; upper tooth longer in forebody but as long as lower and thinner in hindbody, may be pectinated with short intermediate denticles; XI penial chaetae 4−5, weakly sigmoid, with blunt tip; L ≤ 30 mm (Fig. 12.14(37−41)) ..... *Rhyacodrilus punctatus* Hrabě, 1931 [Balkan Peninsula]

14(13) Bifid (and pectinate, if present) chaetae not dilated distally 15

14′ Hair and pectinate chaetae in dorsal bundles, bifid crotchets in ventral bundles; intermediate denticles in pectinates forming a continuous membrane; both pectinate and bifid chaetae the distal portion dilated..... *Rhyacodrilus profundalis* Lastočkin, 1937 [Russia: Lake Umbozero on Kola Peninsula]

15(14) Protrusible pseudopenes present 16

15′ Protrusible pseudopenes absent 18

16(15) Ventral chaetae not pectinate, penial chaetae bifid or blunt-tipped 17

16′ Hair chaetae both smooth and pilose, 4−8 in forebody and gradually fewer posteriorly, absent in last segments; dorsal pectinate chaetae 5−9 in forebody and 1−5 posteriorly, with subequal teeth and 6−11 parallel intermediate denticles; sometimes one main tooth truncated and pectinate; forebody ventral chaetae 6−8, posteriorly 2−5 per segment, all pectinate but with shorter intermediate denticles than dorsal ones; penial chaetae 3−7 per bundle, with distal ends split into several short denticles; pseudopenes protrusible but not always protruded; L = 17−35 mm (Fig. 12.14(27−32)) ..... *Rhyacodrilus hiemalis* Ohtaka, 1995 [Japan]

17(16) Pseudopenes permanently protruded; hair chaetae in II−VIII only, 4−6, long, plus 5−7 pectinate chaetae; ventral crotchets anteriorly 6−8 (10), with slightly longer upper tooth; posteriorly 4−5, with teeth equal; penial chaetae 4−6, bluntly simple-pointed; L ≥ 40 mm (Fig. 12.14(11−15)) ..... *Rhyacodrilus sibiricus* Semernoy, 1971 [Russia: eastern Siberia]

17′ Pseudopenes usually not protruded; hair chaetae present along entire body, in preclitellar segments 3−6, in tail region one; dorsal pectinate chaetae anteriorly 4−7, posteriorly replaced by 2−3 bifid chaetae; ventral crotchets anteriorly 5−8, with slightly longer upper tooth, posteriorly 3−4, upper tooth shorter and much thinner; penial chaetae 4−5, almost straight, with rudimentary upper tooth; L = 8−25 mm ..... *Rhyacodrilus sokolskajae* Semernoy, 1971 [Russia: eastern Siberia]

18(17) Hair chaetae present in several anterior dorsal bundles but lacking in postclitellar segments 19

18′ Hair chaetae present also at least in some postclitellar segments 21

19(18) Pectinate chaetae present at least in preclitellar dorsal bundles 20

19′ No pectinate chaetae. Preclitellar dorsal bundles with 1−2 very finely pilose hair chaetae, none in postclitellar segments; dorsal bifids 2−4 and with subequal teeth in forebody, 2−3 in postclitellar but 4−5 in very last segments, with upper tooth much longer; ventral bifids 2−6, with upper tooth much longer in fore- and hindbody but subequal in midbody; spermathecal chaetae by 1−2, bifid alike somatic chaetae but larger and equipped with glands, upper tooth three times longer than lower; penial chaetae 1−2, parallel in bundle, relatively thick, with blunt tip or reduced upper tooth; L = 6−10 mm; caves ..... *Rhyacodrilus moulis* Achurra & Rodriguez, 2016 [France]

20(19) X ventral chaetae teeth difference in length not increasing; two hair chaetae in dorsal bundles present only in II−V, plus 3−5 pectinate chaetae with thin teeth and shorter, fine intermediate denticles; ventral bundles 4−5 bifid chaetae with upper tooth longer; posteriorly bifid chaetae four; penial chaetae three, with rudimentary teeth; L = 6 mm ..... *Rhyacodrilus inaequalis* (Michaelsen, 1905) [Russia: Lake Baikal and Angara River]

20′ Some anterior dorsal bundles with 1−2, smooth hair chaetae; dorsal pectinates anteriorly 2−3 and posteriorly one, with short and fine intermediate denticles; ventral bifids anteriorly 3−5 and posteriorly 2−3, with upper tooth length two times lower in anterior bundles, the teeth becoming equal posteriorly; X ventral chaetae teeth difference in length three times ventrally at spermathecal pores; XI male pores 2−3 slightly sigmoid, blunt-tipped penial chaetae; groundwater ..... *Rhyacodrilus okamikae* Giani & Rodriguez, 1988 [Spain]

21(18) Dorsal pectinate chaetae not lyriform 22

21′ Dorsal bundles of fore- and midbody with 1−2 (3) smooth hair chaetae (sometimes up to three additional small hairs) and 1−4 pectinates with lyriform apex: slender, symmetrically parallel main teeth bound with a membrane of very thin intermediate denticles; tail region dorsal bundles with bifid chaetae only; ventral bundles 3−8 bifid chaetae anteriorly, 2−3 caudally, with equal teeth or distal tooth longer but thinner; XI penial chaetae 2−5 per bundle, with bent, sharp tip or with two rudimentary teeth; L = 5.5−22 mm (Fig. 12.14(33−36)) ..... *Rhyacodrilus suputensis* Timm, 1990 [southeastern Russia]

22(21) Anterior dorsal bundles 1−4 smooth hair chaetae, midbody 1−2, none in tail segments; dorsal pectinates (intermediate denticles 3−4 or lacking?) also 2−4 in anterior segments, with equal thin teeth or upper tooth longer; anterior ventral bundles 3−6 bifid chaetae with equal teeth or upper tooth slightly longer; lower tooth twice as thick and more curved than the upper; one to three bifids with thicker and more curved lower teeth caudally; XI penial chaetae 3−5, with blunt, slightly curved tip or with reduced upper tooth; L = 8−25 mm ..... *Rhyacodrilus sinicus* Chen (1950) [China]

22′ Dorsal pectinate chaetae with diverging teeth, not lyriform; anterior dorsal bundles 3−8 smooth hair chaetae and 3−7 pectinates, with equal main teeth and several small intermediate denticles; anterior ventral bundles 4−8 bifid chaetae with teeth subequal; dorsal and ventral posterior bifid chaetae upper tooth can be shorter; atria compact, ovoid; XI penial chaetae 2−5 per bundle, with blunt bent tip or with reduced upper tooth, often hardly protruding from male pore aperture; L = 15−35 mm (Fig. 12.14(21−26)) ..... *Rhyacodrilus coccineus* (Vejdovský, 1875) [Holarctic. Australia, Antarctic islands]

23(1) Chaetae at least in anterior bundles with equal teeth or upper tooth longer (although often thinner) 24

23′ Most chaetae, at least in anterior bundles, with shorter and thinner upper tooth; XI penial chaetae with thickened, hollow proximal end and simple, fine, slightly hooked, converging or diverging tips 6−7; ordinary anterior bundle chaetae 2−5, posteriorly 1−3, with upper tooth shorter, thinner; coelomocytes present; L = ∼3 mm; groundwater (Fig. 12.17(44, 45)) ..... *Rhyacodrilus balmensis* Juget, 1959 [France]

24(23) Spermathecal chaetae with grooved, acute distal portion 25

24′ Modified spermathecal chaetae bifid or lacking; blunt or only slightly modified penial chaetae present 26

25(24) Single spermathecal chaetae with slightly dilated and grooved, acute distal portion in X, surrounded by muscular-glandular chaetophore; XI penial chaetae single and bifid-like ordinary chaetae but smaller; the latter dorsally 5−7 in forebody but decreasing to two posteriorly; ventrally 5−8 in forebody, 2−5 in midbody, and 7−8 in very last segments; all bifids with upper tooth 2−3 times longer and thicker; L = 7−8 mm; caves ..... *Rhyacodrilus arenivorus* Achurra & Rodriguez, 2016 [France]

25′ Single (seldom two) grooved spermathecal chaetae with narrow, acute distal portion present in X or also in some neighboring segments; XI penial chaetae 2−4 per bundle, almost straight, blunt or with thicker and strongly curved upper tooth; ordinary chaetae in anterior bundles 3−7, posteriorly 2−6, with upper tooth length 2−3 times lower, difference decreasing posteriorly; dorsal chaetae of XI can be enlarged, with particularly long and wide upper tooth; large coelomocytes abundant; L = 11−13 mm (Fig. 12.18(9−16)) ..... *Rhyacodrilus carsticus* Košel, 1980 [southern Europe]

26(24) Bifid spermathecal chaetae in X (or also in IX and XII), blunt penial chaetae in XI 27

26′ No modified spermathecal chaetae; penial chaetae present, sometimes only slightly modified 28

27(26) Modified spermathecal chaetae in IX, X, and XII, single, upper tooth seven times lower, acute, concave; XI penial chaetae three, sometimes 4−5 per bundle, tips obtusely bifid, converging; anterior and midbody bundles ordinary chaetae 3−6 (7), teeth subequal; ventral and posteriormost dorsal chaetae upper tooth length 2−3 times lower, number decreasing to (0) 2−4 (5); L = 6−7 mm (Fig. 12.18(21−27)) ..... *Rhyacodrilus ardierae* Lafont & Juget, 1993 [France]

27′ Spermathecal chaetae in X only, single, upper tooth very long, cochliform, lower tooth broad, short, at right angle to chaetal axis; XI "penial" chaetae two, teeth length equal, upper tooth thinner; ordinary chaetae with longer upper tooth, anteriorly (6) 8−11, posteriorly 5−8 per bundle; L = ?; groundwater ..... *Rhyacodrilus gernikensis* Giani & Rodriguez, 1988 [Spain]

28(26) Single very large penial chaetae at male pores 29

28′ Several not extra large, blunt penial chaetae at male pores 30

29(28) Distal portion of penial chaetae sickle-shaped, with short tip; all other chaetae with upper tooth length two times lower, 2−6 in anterior bundles and 1−2 posteriorly; living worm white due to abundant coelomocytes; L = 8−10 mm; groundwater, springs, clean lakes, terrestrial soil (Fig. 12.18(44−46)) ..... *Rhyacodrilus falciformis* Bretscher, 1901 [Europe. Invasive in Nearctic]

29′ Distal portion of penial chaetae almost straight but with hooked obtuse tip; all other chaetae with upper tooth somewhat longer, 3−5 in anterior bundles and 1−3 posteriorly; coelomocytes abundant; L = ?; in caves ..... *Rhyacodrilus pigueti* Achurra & Martinsson, 2013 [France]

30(28) Chaetae less numerous, 2−8 per bundle 31

30′ Both ordinary and penial chaetae ∼10 per bundle; several blunt penial chaetae per bundle at male pores; anterior segments 10−13 chaetae, tooth length variable within a bundle; penial chaetae 9−10, with teeth variously rudimentary; L ≥ 10 mm ..... *Rhyacodrilus multiovatus* (Burow, 1932) [Russia: Lake Baikal and Angara River]

31(30) Conical pseudopenes present, often protruded in fixed specimens 32

31′ No pseudopenes; penial chaetae 3−4 (5) with rudimentary teeth; other chaetae similar but of slightly different shape in same bundle, either with equal teeth or upper tooth longer and thinner, (6) 7−8 in anterior and 2−4 in posterior bundles; L = 17−20 mm ..... *Rhyacodrilus stephensoni* Černosvitov, 1942 [eastern Asia]

32(31) XI penial chaetae 3−4 per bundle, with two reduced teeth; male pores medial to penial chaetae; conical pseudopenes can be protruded perpendicularly to body wall; ordinary chaetae 3−5 per bundle, upper tooth slightly longer than proximal but always thinner, with subequal teeth in hindbody; few tiny intermediate denticles in posterior ventral chaetae; L = 9−10 mm ..... *Rhyacodrilus levanidovae* Sokolskaja, 1973 [Russia: Kamchatka Peninsula]

32′ XI penial chaetae 2−5 per bundle, blunt or with rudimentary distal tooth, hidden in body wall; male pores laterad of penial chaetae; conical pseudopenes can be protruded obliquely anteriorly; ordinary chaetae 3−7 per bundle anteriorly and 3−5 in tail region, with upper tooth length subequal to proximal but always thinner; few very tiny intermediate denticles may occur; L = 4−9 mm (Fig. 12.18(47−50)) ..... *Rhyacodrilus komarov*i Timm, 1990 [Japan; southeastern Russia]

Oligochaeta: Tubificida: Tubificidae: *Monopylephorus*: Species

1 Hair chaetae absent 2

1′ Anterior dorsal bundle hair chaetae 1−2, thin (often broken), with distal ends twisted; bifid crotchets 2−4 in anterior dorsal and 2−7 in ventral bundles, fewer posteriorly, with considerably longer and thinner upper tooth; anterior dorsal crotchets often modified as pectinates, with some small intermediate denticles; XI ventral bundles sometimes (but not always) replaced with single sigmoid, acute penial chaetae; L = 15−35 mm; marine littoral and fresh water receiving saline wastes (Fig. 12.13(34−38)) ..... *Monopylephorus irroratus* (Verrill, 1873) [Europe. Nearctic]

2(1) No simple-pointed locomotory chaetae; XI male pore and X spermathecal pore single and midventral; small coelomocytes very abundant; chaetae bifid with sharp equal teeth or upper tooth slightly longer; older chaetae teeth may be worn; anterior bundles with 3−6, posterior ones with 2−4 chaetae; no ventral chaetae in XI; L = 10−60 mm (Fig. 12.19(41−44)) ..... *Monopylephorus rubroniveus* Levinsen, 1884 [cosmopolitan]

2′ II with chaetae simple-pointed in ventral, sometimes also dorsal bundles; in remaining segments chaetae with shorter upper tooth, 3−5 (6) anteriorly and 2−3 in postclitellar bundles; XI without ventral chaetae; male pore in XI single, mid-ventral, as is spermathecal pore in X; small coelomocytes abundant; VI−X with dilated transverse blood vessels; L = 15−70 mm; mostly in polluted water ..... *Monopylephorus limosus* (Hatai, 1898) [eastern Asia. Introduced to Europe]

Oligochaeta: Tubificida: Tubificidae: *Pararhyacodrilus*: Species (excluding Lake Baikal)

1 Hair chaetae present also in midbody; anterior dorsal bundle bifid crotchets 4−5, with equal parallel teeth (without pectination?); posterior bundles 2−3 crotchets, the lower tooth becoming gradually thicker and more curved, but upper one thin, short and erect; ventral chaetae 4−7 in anterior bundles with longer upper tooth but becoming similar to dorsal ones posteriorly; penial chaetae 4−6 per bundle, with simple thin curved tip. L ≤ 20 mm (Fig. 12.14(47−51)).....*Pararhyacodrilus ekmani* (Piguet, 1928) [Sweden]

1′ Hair chaetae present only in II−V; bifid crotchets in all dorsal bundles and in anterior ventral bundles with considerably longer upper tooth; caudally upper tooth becomes equal and even shorter than lower; penial chaetae several per bundle, with simple curved tip, slightly larger than ordinary chaetae; L = ∼6 mm ..... *Pararhyacodrilus palustris* (Ditlevsen, 1904) [Denmark]

Oligochaeta: Tubificida: Tubificidae: *Epirodrilus*: Species

1 Modified genital chaetae present in sexually mature individuals 2

1′ Ventral chaetae at genital pores unmodified or lacking even in mature individuals 3

2(1) Anterior dorsal bundles with 2−3 hair and 3−4 pectinate chaetae with three intermediate denticles, posterior bundles with one hair and 2−3 bifid chaetae with teeth equal; ventral chaetae 4−7 (8) in anterior and 3−4 in posterior bundles, upper tooth longer than lower in anterior ventral chaetae but equal posteriorly; XI at male pores three sigmoid, simple-pointed penial chaetae; L = 6 mm; groundwater. ..... *Epirodrilus slovenicus* Karaman, 1976 [Slovenia]

2′ Anterior dorsal bundles with 1−3 hair and (2) 3−4 pectinate chaetae with 3−5 short intermediate denticles; postclitellar segment hair chaetae diminishing until absent, pectinates decrease to 1−3; ventral bundles (2) 4−6 (7) and 2−5 (6) bifids, respectively, with upper tooth slightly thinner and longer anteriorly and shorter in posterior most segments; XI at male pores penial chaetae (4) 5−6, with blunt slightly curved tip; L = 7−9 mm (Fig. 12.14(42−46)) .....*Epirodrilus moubayedi* Giani et Martínez-Ansemil, 1983 [Turkey; Lebanon; Tunis]

3(1) Anterior dorsal bundles with 2−4 pectinates with slightly shorter or equal upper tooth, many fine, short intermediate denticles, plus 2−3 smooth hair chaetae; anterior ventral chaetae 3−5, often with longer upper tooth; chaetal number decreasing posteriorly while upper tooth becoming slightly shorter; L = 15−20 mm.....*Epirodrilus pygmaeus* (Hrabě, 1935) [central and southern Europe]

3′ Anterior dorsal bundles with 2−5 pectinates with slightly longer, thinner upper tooth, 1−4 short intermediate teeth, plus 1−4 smooth hair chaetae; anterior ventral chaetae 4−6 (8), with longer upper tooth; caudally only bifids with shorter and thinner upper tooth, two per bundle; L = ∼10 mm ..... *Epirodrilus michaelseni* Hrabě, 1930 [Balkan Peninsula; Algeria]

Oligochaeta: Tubificida: Tubificidae: *Ilyodrilus*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent; penial sheaths short, truncated conical; anterior bundles chaetae 4−7, bifids with larger upper tooth; individuals with occasional hair chaetae are described from brackish water in North America; L = 12−20 mm .... *Ilyodrilus frantzi* Brinkhurst, 1965 [Turkey(?). Nearctic, Neotropics]

2(1) No ventral chaetae in XI at male pores 3

2′ Penis sheaths (?) short cylindrical, very thin, not seen in all specimens; ordinary bifid chaetae at male pores in XI(?); all dorsal bundles 1−6 very finely pilose hair chaetae and 3−7 pectinate or palmate chaetae, the latter with curved distal portion and 5−14 intermediate denticles, with length equal to main teeth; anterior bundle ventral chaetae 4−6, with upper tooth slightly longer and thinner; posteriorly decreasing to 2−3, while teeth become subequal but the upper tooth thinner; L = 17 mm ..... *Ilyodrilus sokolskayae* Brinkhurst, 1970 [Russia: Kuril Archipelago]

3(2) Pectinate chaetae present in anterior dorsal bundles; penis sheaths longer than wide, very delicate; anterior dorsal bundles 1−4 smooth hair chaetae and 3−4 pectinates with equal teeth; anterior ventral bundles 3−4 bifid chaetae with slightly longer upper tooth; L = 10−14 mm (Fig. 12.15(38−42)) ..... *Ilyodrilus templetoni* (Southern, 1909) [Holarctic]

3′ No pectinate chaetae; dorsal bundles with 2−5 hair chaetae and 2−4 bifids with longer and thicker upper tooth; ventral chaetae 2−4, with longer and thinner upper tooth; both dorsal and ventral chaetae lacking in XI; penis sheaths truncate conical; L > 4.4 mm .... *Ilyodrilus mesoprostatus* Cui & Wang, 2009 [China: Lake Xingyun]

Oligochaeta: Tubificida: Tubificidae: *Peipsidrilus*: Species

1 Hair chaetae present 2

1′ Hair chaetae absent; penis sheaths in XI thick-walled, length = width, with funicular proximal and fungiform distal end; X often with single thin spermathecal chaetae with fine groove distally; ordinary chaetae 2−6 per bundle, with equal short teeth; L = 6−8 mm (Fig. 12.18(31−35)) ..... *Peipsidrilus pusillus* Timm, 1977 [Europe]

2(1) Penis sheaths as delicate truncated cones; no ventral chaetae at spermathecal and male pores located in X and XI, or VIII and IX, respectively; reproductive system forward shift supposedly connected with architomy (fragmentation); dorsal bundles with 1−6 smooth hair chaetae and 1−4 pectinates, the latter with relatively long and straight teeth and 1−3 slightly shorter intermediate denticles; ventral bifids 1−5, with equal teeth or upper tooth slightly longer, often with tiny intermediate denticle; all three kinds of chaetae present in postclitellar segments but in smaller number; L = ∼6 mm (Fig. 12.15(29−33)) ..... *Peipsidrilus saamicus* (Timm, 1978) [northern Europe]

2′ Penis sheaths short, funicular; anterior dorsal bundles none to three smooth hair and (2) 3−4 (5) pectinate chaetae; the latter with equal teeth and (2) 3−5 rough intermediate denticles; postclitellar segments with hair chaetae diminishing while the pectinates are replaced by bifids, their number decreasing to 1−4 (4); anterior ventral chaetae 3−6 (8), posteriorly 2−5, upper tooth being slightly longer in anterior and shorter in the most posterior bundles; XI at male pores 2−3 ordinary bifids present (but sometimes absent); L = 6−7 mm (Fig. 12.15(12−17)) ..... *Peipsidrilus libanus* (Giani, Martínez-Ansemil, Moubayed & Dia, 1982) [Lebanon, Turkey]

Oligochaeta: Tubificida: Tubificidae: *Tasserkidrilus*: Species (excluding Lake Baikal)

1 Hair chaetae present 2

1′ Hair chaetae absent 5

2(1) Anterior dorsal bundles mostly with several hair chaetae; ventral chaetae without large glands 3

2′ Anterior dorsal bundles with none to one hair chaeta, plus 3−5 pectinates with longer upper tooth and 1−2 intermediate denticles; ventral chaetae 3−5, similarly with longer upper tooth, some may have an intermediate denticle; all ventral chaetae with a large gland; posterior segments with 2−3 bifid chaetae both in dorsal and ventral bundles; penis sheaths with proximal portion funicular, slightly extended main part, sharp ectal end, and lateral ectal aperture; L > 8 mm ..... *Tasserkidrilus kessleri* (Hrabě, 1962) [Russia: Lake Onega]

3(2) Penis sheaths shorter, funicular 4

3′ Penis sheaths tubular, funicular proximally but distally cupped and acute; anterior dorsal bundles 1−4 smooth or finely pilose hair chaetae besides 3−4 pectinates with equal obtuse teeth and 2−4 intermediate denticles slightly shorter than teeth; dorsal hair and pectinate chaetae decrease to one caudally; anterior ventral bundles 3−5, posteriorly 2−3 bifid or pectinate chaetae, with upper tooth longer and thinner than lower, usually with one to three short and thin intermediate denticles; L = 18−22 mm (Fig. 12.15(18−22)) ..... *Tasserkidrilus americanus* (Brinkhurst & Cook, 1966) [northeastern Russia; invasive in Europe. Nearctic]

4(3) Penis sheaths very short funicular, length and width subequal; anterior bundles 1−5 hair chaetae, smooth or finely pilose proximally, plus 2−4 pectinates with equal obtuse teeth and (1) 2−3 intermediate denticles of same length; posteriorly the number of both kinds of dorsal chaetae decreases to 1−2 while pectinates upper tooth becomes longer and the intermediate denticles small; ventral bifid chaetae anteriorly 2−6, posteriorly 1−2, all with longer and thinner upper tooth; L = ∼18 mm (Fig. 12.15(23−28)) ..... *Tasserkidrilus hrabei* (Sokolskaja, 1973) [Russia: Kamchatka]

4′ Penis sheaths funicular, length > proximal width; spermathecal ampulla bipartite; anterior dorsal bundles with 1−2 hair chaetae and 2−4 pectinate chaetae with slightly longer upper tooth and 2−3 intermediate denticles; posteriorly one hair and two bifid chaetae per bundle; ventral chaetae anteriorly 3−4, posteriorly 2−3, with slightly longer upper tooth; L = 20 mm ..... *Tasserkidrilus baicalensis* (Semernoy, 1982) [Russia: Lake Baikal and Angara River in Siberia]

5(1) Chaetae 4−5 per bundle, with teeth equal or upper tooth slightly longer; penis sheaths with sharp, often bent and finely barbed distal appendage and lateral opening; L = 15 mm ..... *Tasserkidrilus variabilis* (Semernoy, 1982) [Russia: Lake Baikal and Angara River in Siberia]

65′ Chaetae 2−6 in anterior bundles, with slightly longer, thinner, straighter upper tooth; 1−3 and with more equal teeth posteriorly; L = 5−10.5 mm (Fig. 12.19(34−36)) ..... *Tasserkidrilus acapillatus* (Finogenova, 1972) [Palaearctic]

Oligochaeta: Tubificida: Tubificidae: *Limnodrilus*: Species (excluding Lake Baikal)

1 All chaetae simple-pointed 2

1′ At least some chaetae bifid 3

2(1) Chaetae 3−5 per bundle, not enlarged or hooked; chloragogen tissue beginning in XI; penis sheaths with funicular proximal and cylindrical distal portion, without distal modifications, length 1.2 times proximal width; L = ∼3 mm (Fig. 12.17(22, 23)) ..... *Limnodrilus simplex* He, Cui & Wang, 2010
[China: Changjiang River]

2′ Preclitellar segments with chaetae two per bundle, particularly large and hooked, with distal portion bent at right angle to axis; postclitellar segments one, smaller; penis sheaths length six times maximum diameter, with wide discoidal distal end; L = 75−130 mm ..... *Limnodrilus dybowskii* (Grube, 1873)
[Russia: Lake Baikal and Enisej River in Siberia]

3(1) Most chaetae, at least in some anterior bundles, with shorter and thinner, or worn down upper tooth 4

3′ Chaetae at least in anterior bundles with equal teeth or upper tooth longer (although often thinner) 5

4(3) Anterior chaetae 3−7 per bundle, with bluntly bifid or (worn down) simple obtuse tip; posteriorly 1−2 chaetae per bundle, with two short teeth, the upper smaller than lower; penis sheaths short, with funicular proximal base and asymmetrically rounded lamelliform distal end; L = 30−50 mm (Fig. 12.17(9−15)) ..... *Limnodrilus amblysetus* Brinkhurst, Qi & Liang, 1990
[China]

4′ Anterior chaetae 5−7 per bundle, with blunt teeth equal or upper tooth shorter; posteriorly 3−5 chaetae with equal teeth, upper one shorter; penis sheath short, with subcylindrical shaft and broad distal end with a lateral appendage (hooded); L = 15−23 mm (Fig. 12.17(16−21)) ..... *Limnodrilus paramblysetus* Wang & Liang, 2001
[China]

5(3) No enlarged chaetae. Penis sheaths almost cylindrical, gradually narrowing toward distal end 6

5′ Chaetae 1−4, mostly two in anterior bundles, 1−2 and much smaller posteriorly, with short equal long teeth; IV−X ventral chaetae extraordinarily large, with blunt teeth; esophagus chloragogen tissue beginning in VI; penis sheaths very short, thick-walled, with funicular proximal base and asymmetrically hooded (with lateral appendage) or rounded triangular lamelliform distal end; L = 80−130 mm (Fig. 12.19(1−5)) ..... *Limnodrilus grandisetosus* Nomura, 1932
[eastern and southern Asia]

6(5) Anterior chaetae with teeth equal or upper tooth slightly longer but not bent at right angle. Penis sheaths length > four times maximum diameter 7

6′ II−IV most chaetae 3−8 per bundle, upper tooth thicker, length ≥ two times lower, bent nearly 90°; teeth becoming gradually equal in subsequent segments; esophagus chloragogen tissue beginning in VI; body tough, tail long and smooth, prolonged segments bearing transverse yellow stripes; penis sheaths small, short cylindrical, length ∼four times maximum width; L = 35−70 mm (Fig. 12.19(6−11)) ..... *Limnodrilus udekemianus* Claparède, 1862
[cosmopolitan]

7(6) Penis sheaths relatively longer, distal end not fungiform 8

7′ Penis sheaths length ∼ five times maximum diameter, with symmetrical fungiform distal end; chaetae with teeth equal, anterior bundles 5−9; esophagus chloragogen tissue beginning in VI; L = 25−50 mm (Fig. 12.19(18−21)) ..... *Limnodrilus profundicola* (Verrill, 1871)
[Holarctic]

8(7) Penis sheaths length >20 times maximum diameter 9

8′ Penis sheaths length 8−14 times maximum diameter, usually slightly curved distally, distal "head" asymmetrical and often equipped with hamulate appendage; chaetae with teeth subequal length, anterior bundles 4−10; esophagus chloragogen tissue beginning in V; tail segments may bear yellow transverse stripes; L = 12−60 mm (Fig. 12.19(12−17)) ..... *Limnodrilus hoffmeisteri* Claparède, 1962
[cosmopolitan]

9(8) Penis sheaths not especially thick-walled 10

9′ Penis sheaths with very thick or double wall 11

10(9) Penis sheaths length usually 20−48 times maximum diameter, with a small triangular distal "head"; anteriormost chaetae 5−10 per bundle, upper tooth slightly longer than proximal; posteriorly chaetae number decreases while teeth become equal; esophagus chloragogen tissue beginning in V; L = 20−60 mm (Fig. 12.19(27−29)) ..... *Limnodrilus claparedianus* Ratzel, 1868
[cosmopolitan]

10′ Penis sheaths length 80−90 times maximum diameter, with a thin spiral appendage and two short digitiform projections on distal "head"; anteriormost chaetae 5−10 per bundle, with upper tooth longer, thinner than proximal; posteriorly chaetae three to four, with equal teeth or upper tooth shorter; L = 15−22 mm (Fig. 12.19(30−33)) ..... *Limnodrilus tortilipenis* Wetzel, 1987
[invasive in Europe. Nearctic]

11(9) Penis sheaths length ≤48 times maximum diameter, double-walled, but thicker external layer lacking near distal end; distal sheath "head" with two solid triangular processes; anteriormost bundles chaetae 4–10, posterior ones fewer, all with upper tooth slightly longer and thinner than proximal; L = 30–80 mm (Fig. 12.19(26)) ..... *Limnodrilus cervix* Brinkhurst, 1963 [invasive in Europe. Nearctic]

11′ Penis sheaths length ≤48 times maximum diameter, thick-walled, distal end curved; distal sheath "head" broad and triangular, asymmetrically on shaft; chaetae up to 10 anteriorly, fewer posteriorly, with upper tooth a little longer and thinner; L = ∼20 mm (Fig. 12.19(22–25)) ..... *Limnodrilus maumeensis* Brinkhurst & Cook, 1966 [invasive in Europe. Nearctic]

Oligochaeta: Tubificida: Tubificidae: *Gianius*: Species

1 Simple-pointed locomotory (not genital) chaetae present, accompanied with bifids with shorter upper tooth 2

1′ No simple-pointed locomotory chaetae; locomotory chaetae of three kinds: anterior chaetae 2–3 with shorter upper tooth, midbody and tail region two simple-pointed, small and sharp ventrally, larger and more obtuse dorsally; XI penial bundles consisting of 4–5 parallel, sigmoid chaetae with simple thin tip; midgut widening only behind clitellum; L = 3–3.5 mm (Fig. 12.17(39–42)) ..... *Gianius anatolicus* Arslan, Timm & Erséus, 2007 [Turkey]

2(1) Modified penial chaetae at male pores present..... 3

2′ No modified genital chaetae; ordinary chaetae at male pores in XI; chaetae with upper tooth shorter than lower, 3–4 in anterior and 2–3 in posterior segments; male pores on porophores; L = ?; groundwater ..... *Gianius labouichensis* (Rodriguez & Giani, 1989) [France]

3(2) At least some penial chaetae bifid 4

3′ All penial chaetae simple-pointed..... 6

4(3) Penial chaetae only bifid; male pores on porophores..... 5

4′ Penial chaetae (2) 4–7, bifid with shorter upper tooth like ordinary chaetae but thicker and straighter, or simple-pointed; ordinary chaetae 3–6 in anterior bundles and 2–3 posteriorly; spermathecae as prolonged cylindrical sacs with a short, narrow duct; L = 1.7–4 mm ..... *Gianius aquaedulcis* (Hrabě, 1960) [Holarctic]

5(4) Male pore with bundle of 4–5 straight penial chaetae with curved distal end, forming an arc; ordinary chaetae upper tooth shorter than lower, 2–5 in anterior, two in posterior segments; spermathecae with stout ducts and elongated, globular ampullae, both fitting to X; L = 1.7 mm..... *Gianius navarroi* Rodriguez & Achurra, 2010 [Spain]

5′ XI penial chaetae 7–8 per bundle, in flabelliform bundles, tips converged, the short distal portion curved; ordinary chaetae three (4) per bundle anteriorly and two beginning from IX, bifid, with upper tooth shorter, thinner than lower; spermathecae with short ducts, and ampullae elongated; spermathecal ampullae asymmetrically arranged, one ampulla in X, the other extending over IX. L = ?..... *Gianius crypticus* (Rodriguez & Giani, 1989) [Spain]

6(3) Penial chaetae thicker and straighter than ordinary chaetae, with short curved, obtuse distal end, four per bundle; ordinary chaetae 2–5 in anterior bundles and 2–3 posteriorly, with shorter upper tooth; L = ∼3 mm; groundwater (Fig. 12.17(52–54))..... *Gianius riparius* (Giani & Martínez-Ansemil, 1981) [southern Europe]

6′ Penial chaetae not thicker than ordinary chaetae, straight, tip thin, simple hooked, four per bundle; ordinary chaetae 2–5 in anterior bundles, upper tooth shorter, thinner than lower, more reduced in anterior segments; L = 4.3–6.6 mm; caves ..... *Gianius cavealis* Juget & DesChâtelliers, 2001 [France]

Oligochaeta: Tubificida: Tubificidae: *Aktedrilus*: Species

1 Penis sheaths curved..... 2

1′ Penis sheaths narrow conical, more or less straight, with expanded proximal end; spermathecal duct simple; spermatozoa in spermatheca arranged in bundle; chaetae 3–6 per bundle, upper tooth smaller than lower; L = 3–4 mm; groundwater ..... *Aktedrilus argatxae* Giani & Rodriguez, 1988 [Spain]

2(1) Spermathecal duct not telescopic 3

2′ Penis sheaths cornuiform, with expanded proximal end; spermathecal duct telescopic; sperm in ampulla as amorphous mass; chaetae 3−6 in anterior bundles, none to two in postclitellar segments, bifid with upper tooth slightly shorter and thinner; L = 4−6 mm; groundwater (Fig. 12.17(51)).....*Aktedrilus ruffoi* Sambugar, Giani & Martínez-Ansemil, 1999 [Italy]

3(2) Penis sheaths long, conical, curved with asymmetrical proximal dilatation; spermathecal duct vestibule suboval; spermatozoa in spermatheca as amorphous mass; chaetae 3−5 per bundle, with smaller upper tooth; L = 3−4 mm (Fig. 12.17(49, 50)) ..... *Aktedrilus yacoubii* Martin & Bourghous, 2012 [Morocco]

3′ Penis sheaths short truncated cones; spermathecal duct not telescopic, with slightly dilated ectal end; sperm in ampulla arranged in bundle; chaetae 4−7 in anterior and 4−5 in posterior bundles, with shorter upper tooth; L = 3−4 mm; brackish water ....*Aktedrilus svetlovi* Finogenova, 1976 [Caspian Sea]

Oligochaeta: Tubificida: Tubificidae: *Aberrantidrilus*: Species

1(2) Penial chaetae at male pores in XI thickened 2

1′ Penial chaetae slender (1.5 μm thick), slightly sigmoid, with thin sharp tip; ordinary chaetae 2−5 anteriorly and three posteriorly, with upper tooth shorter, much thinner than lower; L = ?; groundwater .....*Aberrantidrilus subterraneus* (Rodriguez & Giani, 1989) [Spain]

2(1) Penial chaetae very large (five to seven μm thick), lanceolate, slightly curved distally, with simple sharp tip; ordinary chaetae 2−7 (7) in anterior and 2−4 in posterior segments; anterior and all ventral posterior chaetae bifid with slender and subparallel teeth, upper tooth somewhat shorter and thinner than lower; many posterior dorsal chaetae with upper tooth reduced or lacking; L = ∼5 mm; groundwater (Fig. 12.17(55−58)) ..... *Aberrantidrilus cuspis* (Erséus & Dumnicka, 1988) [southern Europe]

2′ Penial chaetae large (3−3.5 μm thick), with upper tooth much longer and strongly curved; ordinary chaetae 2−5 anteriorly and 1−3 posteriorly, with equal teeth or the upper tooth slightly shorter; L = 4.5 mm; groundwater .... *Aberrantidrilus stephaniae* Martin, 2015 [France]

Oligochaeta: Tubificida: Tubificidae: *Spiridion*: Species

1 Penial chaetae thin and sigmoid, with simple hooked tip, 4−11 per bundle; ordinary chaetae (1) 2−5 (6), with shorter upper tooth; atria consisting of a small oval ampulla covered with prostate tissue, and a long, eversible pseudopenis often protruding from male pore; L = 3−4 mm; groundwater.....*Spiridion phreaticola* (Juget, 1987) [France]

1′ Penial chaetae thin, straight, with short arcuate end and thin, simple tip, up to six per bundle; ordinary chaetae with much smaller upper tooth, anterior bundles 3−5, posteriorly their number gradually decreasing to one; L = 5−10 mm; brackish water ....*Spiridion insigne* Knöllner, 1935 [Europe]

Oligochaeta: Tubificida: Tubificidae: *Bothrioneurum*: Species

1 Foremost chaetae upper tooth thinner, length ∼two times lower, the difference gradually disappearing posteriorly; no enlarged chaetae; anteriorly 3−5 chaetae per bundle, posteriorly two; chloragogen tissue beginning on esophagus obscure; asexual reproduction by architomy (fragmentation) common, sexually mature individuals rare; mature individuals with modified penial chaetae hidden inside body at male pores in IX or XI, 4−6 per bundle, with thick curved upper tooth, small lower tooth split into several denticles; no spermathecae; external stalked, fusiform spermatophores attached to genital segments during copulation; L = 20−35 mm (Fig. 12.18(1−4)) .... *Bothrioneurum vejdovskyanum* Štolc, 1886 [cosmopolitan]

1′ Chaetae with longer upper tooth, 3−8 in anterior and 2−5 in posterior segments; ventral bundles of V−VI 1−3 thickened or giant chaetae with much longer and thicker upper tooth; small intermediate denticles may occur, main teeth tips may be split; giant chaetae medium portion often with longitudinal ribs; glands attached to chaetal sacs; XI penial chaetae two, with hooked blunt tips; no spermathecae; L = 3−7.5 mm; terrestrial..... *Bothrioneurum grandisetosum* Wang, Xie & Liang, 2000 [China]

Oligochaeta: Tubificidae: Genera (Lake Baikal)

Modified after Semernoy (2004).

1 No palmate chaetae 2

1′ Dorsal bundles 3−5 hair chaetae and 4−7 palmate chaetae, with a broad web between long teeth; ventral bundles consist of 4−5 bifid crotchets with subequal teeth; reproductive organs unknown; L = 15 mm ..... ***Psammoryctides***(?), incertae sedis

2(1) Sperm in spermathecae amorphous, not organized into spermatozeugmata 3

2′ Sperm in spermathecae organized into spermatozeugmata 9

3(2) No compact prostate glands on atria 4

3′ Compact prostate glands present 8

4(3) Diffuse prostate glands on atria present 5

4′ Prostate glands completely lacking ..... ***Svetlovia*** **[p. 435]**

5(4) Atrium covered with diffuse prostatic glands, in one or more layers; large coelomocytes present; modified penial chaetae present; spermathecal duct short 6

5′ Atrium diffuse prostatic glands concentrated distally; vas deferens strongly dilated medially; penis conical; anterior dorsal bundles with 3−5 smooth hair chaetae and 4−5 pectinate chaetae with 2−3 fine intermediate denticles; postclitellar segments both hair and pectinate chaetae two; ventral chaetae 2−3, forebody with longer upper tooth; no ventral chaetae in XI; L = 1.8−2 mm; sublittoral ..... *Lymphachaeta pinnigera* Snimschikova, 1982 [Lake Baikal]

6(5) Distal portion of atrium opening directly or with a short duct into male pore, sometimes protruding as a pseudopenis 7

6′ Male ducts terminating with efferent duct and soft penis in penial sac ..... ***Hrabeus*** **[p. 435]**

7(6) Spermathecae connecting with digestive tract ..... ***Pararhyacodrilus*** **[p. 436]**

7′ No connection between spermathecae and digestive tract ..... ***Rhyacodrilus*** **[p. 436]**

8(3) Atrium distally with two compact prostate glands; chaetae uniform, with slightly shorter upper tooth, (2) three to four in preclitellar and 2−3 in postclitellar bundles; XI modified penial chaetae (but of spermathecal type?) single, slightly sigmoid, distally with a long groove, acute; L = 3.2 mm; profundal ..... *Phallobaikalus gladiiseta* (Martin & Brinkhurst, 1998)

8′ Atrium proximally with one large compact prostate gland; dorsal and ventral chaetae uniform, 4−7 and with shorter or rudimentary upper tooth (seldom simple) in foremost bundles, two; postclitellar bundles mostly simple; XI modified penial (but of spermathecal type?) chaetae single, sigmoid, with a short, distal cochliifrom groove; all chaetal bundles with a large accessory gland; L = 6−11 mm; profundal and abyssal (Fig. 12.20(23−25)) ..... *Rhyacodriloides abyssalis* Čekanovskaja, 1975

9(2) Modified genital chaetae present 10

9′ Modified genital chaetae absent 12

10(9) Spermathecal chaetae in X only 11

10′ Genital chaetae of "spermathecal" type both in X and XI ..... ***Haber*** **[p. 437]**

11(10) Body surface smooth; no hair chaetae; spermathecal chaetae thin, acute, distally grooved; thin-walled penial sheaths usually present ..... ***Isochaetides*** [in part; **p. 437**]

11′ Body densely armored with small dark papillae; dorsal bundles with 1−4 hair chaetae and up to four very small, obscure bifid chaetae among papillae; anterior segments ventral bundles with two chaetae, one bifid with shorter upper tooth, the other simple; spermathecal chaetae 1−2, either aciculate or with distal groove; no penial sheaths; L = 23−50 mm. Records from Lake Baikal are probably *Baikalodrilus* spp. confused with this species ..... *Embolocephalus velutinus* (Grube, 1879) [Palaearctic]

12(9) Penial sheath present; body wall smooth 13

12′ Penial sheath absent; body wall smooth or armored with papillae 17

13(12) Penis sheaths short conical, symmetrical 14

13′ Penis sheaths of different shape 15

14(13) Penis sheaths with thick wall, proximal end turned-up; forebody chaetae 5−8 per bundle, with teeth equal or upper tooth longer; L ≥ 6 mm; profundal ..... ***Isochaetides*** [in part; **p. 437**]

14′ Penis sheaths with thin wall; chaetae with shorter or rudimentary upper tooth or simple, in some anteriormost bundles 2−3 per bundle, most bundles single; VI−IX ventral chaetae becoming gradually very large, hamulate and smaller again posteriorly; dorsal chaetae smaller that ventral; L = 36−38 mm; littoral and sublittoral (Fig. 12.20(51−55)) ..... *Lycodrilides schizochaetus* (Michaelsen, 1901) emend. Hrabě, 1982 [Lake Baikal, Angara and Enisej Rivers]

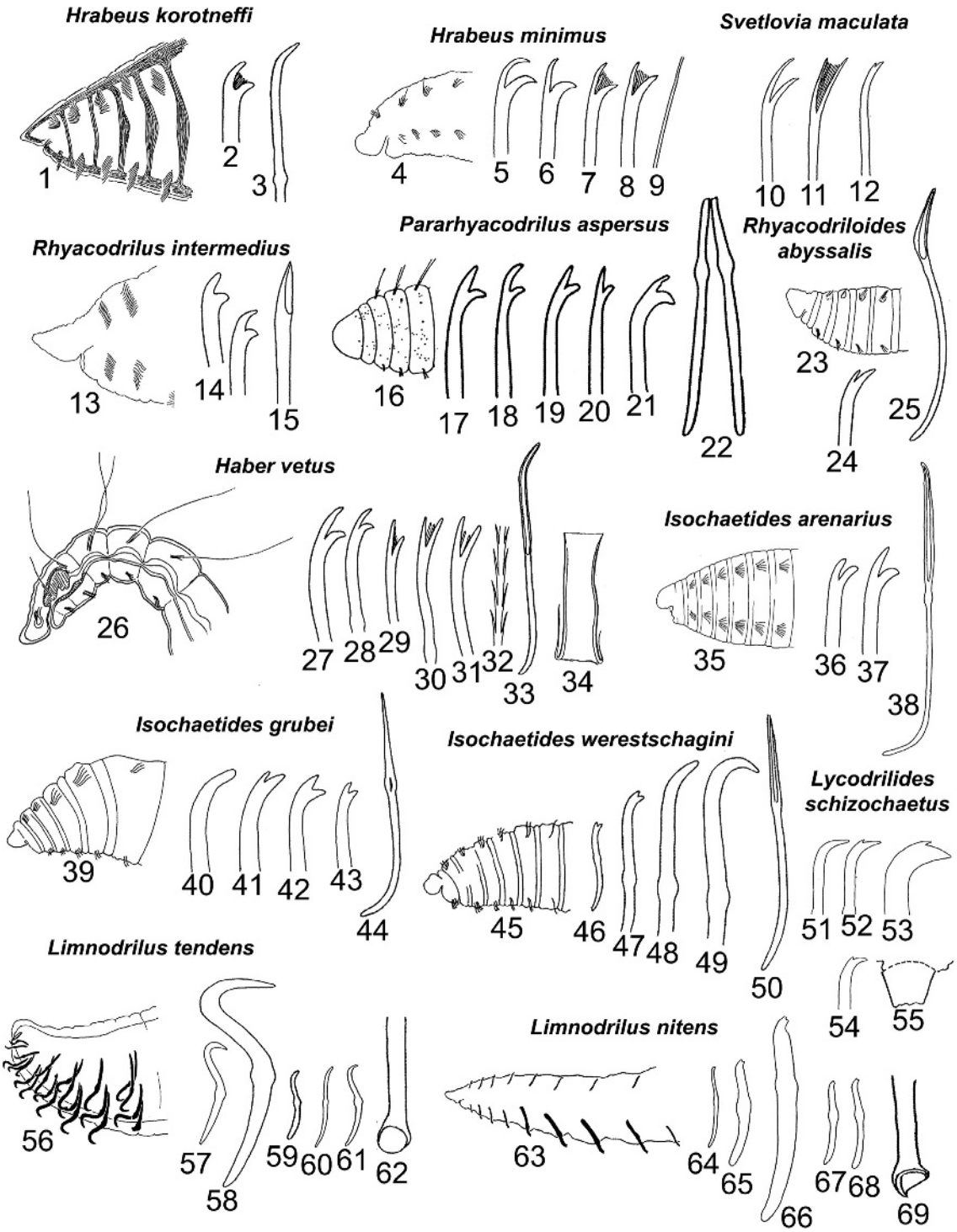


FIGURE 12.20 Tubificidae from Lake Baikal I: (1–3): *Hrabeus tortus*: (1) anterior end, (2) ordinary chaeta, (3) penial chaeta; (4–9): *Hrabeus minimus*: (4) anterior end, (5, 6): anterior ventral chaetae, (7, 8) pectinate chaetae, (9) hair chaeta; (10–12): *Svetlovia maculata*: (10) anterior ventral chaeta, (11) pectinate chaeta, (12) penial chaeta; (13–15): *Rhyacodrilus intermedius*: (13) anterior end, (14) anterior chaetae, (15) penial chaeta; (16–22): *Pararhyacodrilus aspersus*: (16) anterior end, (17, 18) anterior ventral chaetae, (19, 20) anterior dorsal chaetae, (21) posterior chaeta, (22) penial bundle; (23–25): *Rhyacodriloides abyssalis*: (23) anterior end, (24) ordinary chaeta, (25) penial chaeta; (26–34): *Haber vetus*: (26) anterior end, (27, 28) anterior ventral chaeta, (29–31) pectinate chaetae, (32) hair chaeta, (33) genital chaeta, (34) penis sheath; (35–38) *Isochaetides arenarius*: (35) anterior end, (36, 37) anterior chaetae, (38) spermathecal chaeta; (39–44): *Isochaetides grubei*: (39) anterior end, (40–43): anterior chaetae, (44) spermathecal chaeta; (45–50): *Isochaetides werestschagini*: (45) anterior end, (46–48) anterior chaetae, (49) posterior chaeta, (50) spermathecal chaeta; (51–55): *Lycodrilides schizochaetus*: (51–53) anterior chaetae, (54) posterior chaeta, (55) penis sheath; (56–62): *Limnodrilus tendens*: (56) anterior end, (57, 58) anterior ventral chaetae, (59, 60) anterior dorsal chaetae, (61) posterior chaeta, (62) penis sheath; (63–69): *Limnodrilus nitens*: (63) anterior end, (64–66) anterior ventral chaetae, (67, 68) anterior dorsal chaetae, (69) penis sheath.

15(13) Penis sheaths short, distal end asymmetrical without perpendicular plate 16

15′ Penis sheaths mostly long, gradually narrowing distally, with a more or less perpendicular small plate ..... ***Limnodrilus*** **[p. 438]**

16(15) Penes thin; penis sheaths funicular, annular or tubular, usually with distal opening lateral or oblique ..... ***Tasserkidrilus*** **[p. 439]**

16′ Penes ampulliform; penis sheaths short conical or annular, with distal opening oblique ..... ***Lamadrilus*** **[p. 441]**

17(12) Body wall usually armored with epidermal papillae and/or adhered foreign particles; papillae often lacking on prostomium and on I–II which can be retracted 18

17′ Body wall smooth 19

18(17) No organic "crystals" in atria; anterior dorsal bundles with stiff, curved hair chaetae and much thinner pectinate chaetae; anterior ventral chaetae bifid with longer upper tooth; tail region both dorsal and ventral bifid chaetae strongly curved, with thick lower and much thinner and shorter upper tooth; L = 15–40 mm; not in Lake Baikal proper but in small connected lakes (Fig. 12.11(10–13)) ..... *Spirosperma ferox* Eisen, 1879) [Holarctic]

18′ One or several prolonged, transparent, crystal-like organic rods in atria or (seldom) attaching to atria ..... ***Baikalodrilus*** **[p. 441]**

19(17) Atria short, cylindrical, immediately transiting into fusiform or cylindrical penes enclosed into smooth-walled penial sac; vasa deferentia not long, with uniform structure; spermathecal pores dorsolateral, closely after the dissepiment 10/11; anterior bundles both hair and pectinate chaetae 2–3 per bundle, pectinates with long thin teeth and 4–5 fine intermediate denticles; anterior ventral chaetae four, with longer upper tooth; number and length difference decreasing posteriorly; X spermathecal pores with only 1–2 bifid chaetae; chaetal follicles glandular; L = 8 mm; all depth zones ..... *Burchanidrilus minutus* (Čekanovskaja, 1975) [Lake Baikal]

19′ Atria clavate, narrowing in distally; penes prolonged, with thick finely scabrous walls, penial sac with ring formed from an internal fold; vasa deferentia long and bipartite, distal portion wider, not ciliated, appearing goffered; spermathecal pores lateral to chaetal line; anterior dorsal bundles with 1–2 finely pilose hair chaetae and 2–3 pectinate chaetae; anterior ventral chaetae 2–3, with longer upper tooth; posteriorly two, with upper teeth becoming gradually thinner and shorter; L = 10–20 mm; isolated lagoons, shallows, and polluted zones (Fig. 12.16(26–31)) ..... *Tubifex tubifex* (Müller, 1774) [cosmopolitan]

Oligochaeta: Tubificidae: *Svetlovia*: Species (Lake Baikal)

1 No penial chaetae. Spermathecae compact 2

1′ Penial chaetae present, 4–5 per bundle, simple-pointed or with rudimentary upper tooth; spermathecae bipartite; dorsal bundles 5–12 thin hair chaetae and 4–10 pectinate chaetae with long thin, subparallel teeth; ventral chaetae 3–6, with longer upper tooth; body wall armored with fine papillae and adhering substrate particles; anterior shift of genital system by one or two segments in some individuals; L ≤ 10 mm (Fig. 12.20(10–12)) ..... *Svetlovia maculata* Čekanovskaja, 1975 [Lake Baikal]

2(1) Hair chaetae pilose, 4–5 per bundle in anterior segments; anterior pectinate chaetae 4–5, with short teeth and 3–4 intermediate denticles; ventral chaetae 4–5, with longer upper tooth and 1–2 small intermediate denticles; body wall scabrous, with small brown spots of secretion; sublittoral ..... *Svetlovia majusculata* Snimschikova, 1987 [Lake Baikal]

2′ Hair chaetae smooth, 4–5 per bundle in anterior segments; pectinate chaetae 4–5 in anterior segments, equal teeth and several intermediate denticles; posterior segments three, with shorter teeth; anterior ventral chaetae 5–6, with longer upper tooth; posteriorly three; body wall opaque, with granulated cuticle; sublittoral ..... *Svetlovia golyschkinae* Snimschikova, 1987 [Lake Baikal]

Oligochaeta: Tubificidae: *Hrabeus*: Species (Lake Baikal)

1 No hair chaetae 2

1′ Hair chaetae present but only in II–V, one per bundle, short and thin; 4–6 pectinate chaetae with thin teeth and serrate web between them; ventral chaetae 7–9, dorsal chaetae from V on 6–8, with teeth often of equal length, but the upper tooth almost twice as thin as lower; penial chaetae three, with rudimentary upper tooth; penis fusiform, in narrow penial sac; L ≥ 2 mm; littoral (Fig. 12.20(4–9)) ..... *Hrabeus minimus* Semernoy, 2004 [Lake Baikal]

2(1) Penial sac short 3

2′ Penial sac very long; prostomium small, acute; body wall and dissepiments very musculous; dorsal and ventral chaetae up to 10 per bundle, uniform, pectinate, longer upper tooth, with short intermediate denticles or web; penial chaetae up to 10 per bundle but simple; L = 30–65 mm; sublittoral ..... *Hrabeus korotneffi* (Michaelsen, 1905) [Lake Baikal, Angara and Enisej Rivers]

3(2) Penial chaetae with reduced upper tooth, 2−3; vas deferens wide; dorsal and ventral chaetae 5−7 per bundle, uniform, bifid, teeth equal or upper tooth slightly longer; L ≥ 10 mm; littoral ..... *Hrabeus gratus* Semernoy, 2004 [Lake Baikal]

3′ Penial chaetae simple, several per bundle; vas deferens narrow; dorsal and ventral chaetae 7−8 (9), uniform, upper tooth slightly longer, generally with abruptly bent tip; L = 13 mm; littoral (Fig. 12.20(1−3)) ..... *Hrabeus tortus* Semernoy, 2004 [Lake Baikal]

Oligochaeta: Tubificidae: *Pararhyacodrilus*: Species (Lake Baikal)

1 Smooth hair chaetae present in II−VIII, 1−2 per bundle, 3−4 bifid crotchets, upper tooth length twice that of the lower; anterior ventral bundles with similar bifid crotchets 3−4; posterior segments the number decreases to two, becoming longer, thicker, more curved, while upper tooth becomes smaller; penial chaetae two, with rudimentary teeth; body wall opaque, covered with fine grains of brown secretion; large coelomocytes present; L = 4−6 mm; littoral (Fig. 12.20(16−22)) ..... *Pararhyacodrilus aspersus* Snimschikova, 1986 [Lake Baikal]

1′ No hair chaetae; bifid chaetae five per bundle, upper tooth length 1.5 times that of the lower; penial chaetae two, teeth rudimentary; reproductive apparatus shifted forward for one segment (spermathecae in IX, male pores in X); body wall smooth, dissepiments thickened; large coelomocytes not observed; L ≥ 6 mm; abyssal ..... *Pararhyacodrilus confusus* Semernoy, 2004 [Lake Baikal]

Oligochaeta: Tubificidae: *Rhyacodrilus*: Species (Lake Baikal)

1 Worms ≤40 mm long 2

1′ Worms >40 mm long, thick-bodied 11

2(1) Hair chaetae present 3

2′ Hair chaetae absent 7

3(2) Pseudopenes absent 4

3′ Pseudopenes present 6

4(3) Efferent duct of atrium thin-walled, not muscular 5

4′ Efferent duct of atrium muscular; hair chaetae only in II−V, by two plus 3−5 pectinate chaetae with thin teeth and short, fine intermediate denticles; ventral bundles 4−5 bifid chaetae with longer upper tooth; posteriorly bifid chaetae four; penial chaetae three, with rudimentary teeth; L = 6 mm; littoral ..... *Rhyacodrilus inaequalis* (Michaelsen, 1905) [Lake Baikal and Angara River]

5(4) Hair chaetae in dorsal bundles of most segments, anteriorly 3−5, smooth, 3−7 pectinate chaetae with long teeth and intermediate denticles; anterior ventral chaetae 4−6, with subequal teeth; caudally 2−3 bifid chaetae per bundle, with slightly shorter, thinner upper tooth; penial chaetae 2−3, the hooked distal end simple or with rudimentary teeth; atrium efferent duct short, simple; L = 15−35 mm; littoral (Fig. 12.14(21−26)) ..... *Rhyacodrilus coccineus* (Vejdovský, 1875) [Holarctic. Australia, Antarctic islands]

5′ Hair chaetae only in forebody (II−VII), 3−4 per bundle, short and thin; anterior pectinate chaetae three, with longer upper tooth; ventral chaetae 3−4, with equal teeth or upper tooth slightly longer; posterior chaetae 1−4, with shorter upper tooth; penial chaetae three per bundle, with rudimentary teeth; atrium efferent duct relatively long, opening on a glandular tubercle; L = 8 mm; littoral ..... *Rhyacodrilus brevis* Semernoy, 2004 [Lake Baikal]

6(3) Hair chaetae along whole body, preclitellar segments three to four, tail region one; dorsal pectinate chaetae anteriorly 4−6, posteriorly replaced by 2−3 bifid chaetae; ventral crotchets anteriorly 5−8, with slightly longer upper tooth; posteriorly 3−4, upper tooth shorter; penial chaetae four, with rudimentary upper tooth; pseudopenis protrusible but may not be; L = 20−22 mm; bays and isolated lagoon ..... *Rhyacodrilus sokolskajae* Semernoy, 1971 [Lake Baikal; Amur River]

6′ Hair chaetae in II−VIII only, 4−6, long, plus 5−7 pectinate chaetae; ventral crotchets anteriorly 6−8 (10), slightly longer upper tooth; posteriorly 4−5, with equal teeth; penial chaetae 4−6, bluntly simple; pseudopenis permanently protruded; L ≥ 40 mm; in isolated lagoons (Fig. 12.14(11−15)) ..... *Rhyacodrilus sibiricus* Semernoy, 1971 [Lake Baikal; Transbaikalia]

7(2) Atrium tubular or sacculate 8

7′ Atrium ampulla oval or pyriform 9

8(7) Atrium tubular, distal portion thick-walled, muscular; vas deferens narrow; anterior dorsal and ventral chaetae 4−5 per bundle; ventral ones bifid, slightly longer upper tooth, dorsal bundles with bifid and pectinate chaetae together; penial chaetae 2−3, with rudimentary upper tooth; littoral ..... *Rhyacodrilus korjakovi* Semernoy, 2004 [Lake Baikal]

8′ Atrium short tubular or sacculate, distal portion muscular; vas deferens wide; dorsal and ventral chaetae similar, bifid, upper tooth longer or equal to lower, 4−9 per bundle; some with 2−3 intermediate denticles; penial chaetae 2−5, with rudimentary upper tooth; body wall and dissepiments muscular; L = 25 mm; abyssal ..... *Rhyacodrilus vasalatus* Semernoy, 2004 [Lake Baikal]

9(7) Atrium with pyriform ampulla and not very short efferent duct 10

9′ Atrium with suboval oval ampulla and very short efferent duct; dorsal and ventral chaetae similar, mostly with equally long teeth but with considerably longer upper tooth in 1−2 chaetae of every bundle; anterior dorsal bundles with 3−7, anterior ventral bundles with 5−8, posterior bundles with three chaetae; penial chaetae 2−3, with rudimentary teeth; L = 16 mm ..... *Rhyacodrilus isossimovi* Čekanovskaja, 1975 [Lake Baikal]

10(9) Atrium with protrusible pseudopenis; chaetae uniform, upper tooth mostly longer than lower, 4−5 per bundle in anterior segments; penial chaetae two, with rudimentary teeth; L ≥ 10 mm; sublittoral and profundal ..... *Rhyacodrilus propus* Semernoy, 2004 [Lake Baikal]

10′ No pseudopenis; chaetae similar in dorsal and ventral bundles but slightly different shape in same bundle, either with equal teeth or with longer, thinner upper tooth, (6) 7−8 in anterior and 2−4 in posterior bundles; penial chaetae 3−4 (5), with rudimentary teeth; L = 17−20 mm; littoral and sublittoral ..... *Rhyacodrilus stephensoni* Černosvitov, 1942 [eastern Asia]

11(1) Modified genital chaetae only in XI as penial chaetae with rudimentary teeth; atrium with suboval ampulla and narrower duct 12

11′ IX, X, and XII with ventral chaetae of mature individuals modified as genital chaetae of spermathecal type, with sharp, cochliiform apex, hidden in muscular sacs, 1−4 per bundle; XI penial chaetae 6−7, bifid, with tooth shorter than in locomotory chaetae; latter similar in anterior dorsal and ventral bundles, with longer upper and thicker lower tooth, 12−14; some anteclitellar chaetae with reduced lower tooth; posterior segments with teeth gradually becoming equal in length; atrium long, tubular; male pores on muscular tubercles; L = 50 mm; littoral (Fig. 12.20(13−15)) ..... *Rhyacodrilus intermedius* Semernoy, 2004 [Lake Baikal]

12(11) Anterior segments ≤15−16 chaetae per bundle; atrial efferent duct not longer than ampulla ..... *Rhyacodrilus multispinus* (Michaelsen, 1905) [Lake Baikal]

12′ Anterior segments 10−13 chaetae, similar in dorsal and ventral bundles, the tooth length rate variable within a bundle; penial chaetae 9−10, with teeth variously rudimentary; atrial efferent duct longer than ampulla; L ≥ 10 mm; littoral ..... *Rhyacodrilus multiovatus* (Burow, 1932) [Lake Baikal and Angara River]

Oligochaeta: Tubificidae: *Haber*: Species (Lake Baikal)

1 Hair chaetae ≥2 mm in midbody, pilose, one per bundle; pectinate chaetae only in anterior dorsal bundles, 1−3, with long teeth and two intermediate denticles; postclitellar dorsal bundles single bifid chaetae only; ventral chaetae with longer upper tooth, in forebody 4−6, in mid- and hindbody single; X and XI modified genital chaetae single, slightly sigmoid, grooved distally; atrial duct long, tubular; short penis sheaths present, with turned-up collar distally; L = 25 mm; shallow bays (Fig. 12.20(26−34)) ..... *Haber vetus* (Semernoy, 1982) [Lake Baikal]

1′ Hair chaetae not elongate, smooth, 1−2; forebody dorsal pectinate chaetae 3−4, with thin, long teeth and ≤ six thin, slightly shorter intermediate denticles; replaced by two bifid chaetae postclitellum; ventral bundles 3−5 bifid chaetae with slightly shorter upper tooth; atrial duct short; no penis sheath; penis with thickened hypodermal walls; L = 10 mm; interstitial ..... *Haber hubsugulensis* (Semernoy, 1980) [Lake Baikal; Lake Hubsugul]

Oligochaeta: Tubificidae: *Isochaetides*: Species (Lake Baikal)

1 Modified genital chaetae present 2

1′ Modified genital chaetae absent; penis sheaths with thick wall, proximal end turned-up; forebody chaetae 5−8 per bundle, with teeth equal or upper tooth longer; L ≥ 6 mm; profundal ..... *Isochaetides distinctus* Semernoy, 2004 [Lake Baikal]

2(1) All locomotory (not spermathecal) chaetae bifid 3

2′ Bifid and simple-pointed locomotory chaetae present 10

3(2) Dissepiments uniformly thin 4

3′ Anterior dissepiments thickened, fibrous 7

4(3) Distal end of penis simple 5

4′ Distal end of penis with special structures 6

5(4) Penis fusiform or subcylindrical; atrial duct short; chaetae 4−9 per bundle in forebody and 3−4 posteriorly, teeth length rate may vary in a bundle, from upper tooth longer to shorter than lower; L= 25−38 mm ..... *Isochaetides baicalensis* (Michaelsen, 1901) [Lake Baikal and Angara River]

5′ Penis prolonged conical; atrial duct long; chaetae 5−9 per bundle, teeth length rate may vary in a bundle, from upper tooth longer to shorter than the lower; L = 15−35 mm (Fig. 12.20(35−38)) ..... *Isochaetides arenarius* (Michaelsen, 1926) [Lake Baikal and Angara River]

6(4) Penis cylindrical, with small chitinized "cap"; chaetae 5−6 per bundle, upper tooth length ≤ lower; L = 8 mm; profundal ..... *Isochaetides peniacerus* Semernoy, 2004 [Lake Baikal]

6′ Penis cylindrical or conical, apically narrow, with thickened muscular walls; chaetae 5−6 per bundle, upper tooth shorter than lower; L = 5 mm; sublittoral ..... *Isochaetides durus* Semernoy, 2004 [Lake Baikal]

7(3) Spermathecal chaetae in follicles with accessory glands 8

7′ Spermathecal chaetae in follicles without accessory glands 9

8(7) Spermathecal chaetae follicles with single, lobate accessory gland; chaetae 4−7 per bundle, upper tooth length ≤ of lower; L = 6−30 mm; littoral ..... *Isochaetides septatus* Semernoy, 2004 [Lake Baikal]

8′ Spermathecal chaetae follicles with two suboval accessory glands; chaetae 6−7 (8) per bundle, upper tooth length ≤ of lower; L = 20 mm; littoral and sublittoral ..... *Isochaetides adenodicystis* Semernoy, 1982 [Lake Baikal]

9(7) Penis distal end broad, sheath simple cylindrical; chaetae 5−7 per bundle, upper tooth length ≤ of lower; L = 6−10 mm ..... *Isochaetides compactus* Semernoy, 2004 [Lake Baikal]

9′ Penial sheath turned up into two layers, telescopic; chaetae 5−7 per bundle, upper tooth length ≤ lower; littoral ..... *Isochaetides duopenialis* Semernoy, 2004 [Lake Baikal]

10(2) Most chaetae are simple, but anteriormost segments may also have bifid chaetae with equal, short teeth or shorter, thinner upper tooth; II chaetal number per bundle 4−8, III−VIII 1−2, posterior only one, maximum size in midbody; spermathecal chaetae aciculate, distally hollow; penis conical or ovoid, with or without thin sheath; spermatozeugmata tapelike; L = 25−32 mm; littoral and sublittoral (Fig. 12.20(39−44)) ..... *Isochaetides grubei* (Michaelsen, 1905) [Lake Baikal]

10′ Anteriormost segments chaetae bifid with short teeth, 3−6 per bundle; from about VI simple-pointed, longer and thicker, 1−2 per bundle; tail region with single thick chaetae, distally strongly curved; spermathecal chaetae distally grooved; penis ovoid, with thin sheath; spermatozeugmata lanceolate; L = 20−22 mm; littoral and sublittoral (Fig. 12.20(45−50)) ..... *Isochaetides werestschagini* Akinschina & Snimschikova, 1991 [Lake Baikal]

Oligochaeta: Tubificidae: *Limnodrilus*: Species (Lake Baikal)

1 Dorsal and ventral chaetae uniform, bifid, not enlarged, anterior segments 2−8 per segment 2

1′ Chaetae simple or with rudimentary teeth; preclitellar bundles mostly two, rearwards one; preclitellar ventral bundles enlarged (giant) chaetae; penis sheaths relatively short, slightly dilated at ends, with suboval distal plate 3

2(1) Penis sheaths relatively short, with suboval distal plate; esophagus chloragogen tissue beginning from VI; L = 10−50 mm; bays and isolated lagoons (Fig. 12.19(18−21)) ..... *Limnodrilus profundicola* (Verrill, 1871) [Holarctic]

2′ Penis sheaths long, distally narrowing and slightly bent, with strongly asymmetrical distal plate; esophagus chloragogen tissue beginning from V; L = 20−60 mm; bays and isolated lagoons (Fig. 12.19(12−17)) ..... *Limnodrilus hoffmeisteri* Claparède, 1862 [cosmopolitan]

3(1) Simple-pointed and bifid chaetae present; postclitellar portion of body very thin 4

3′ All chaetae simple-pointed, in preclitellar segments two per bundle, postclitellar one; preclitellar ventral chaeta particularly large, hamulate, with distal portion bent at right angle to chaetal axis; L = 75−130 mm ..... *Limnodrilus dybowskii* (Grube, 1873) [Lake Baikal and Enisej River in Siberia]

4(3) II−III ventral chaetae two per bundle, simple-pointed or with rudimentary teeth; IV−X ventral chaetae large, mostly simple-pointed but some with rudimentary upper tooth, strongly hooked distally; preclitellar dorsal chaetae 2−3, postclitellar chaetae one, mostly simple-pointed, not enlarged; L ≤ 60 mm (Fig. 12.20(56−62)) ..... *Limnodrilus tendens* (Semernoy, 1982) [Lake Baikal]

4′ II ventral chaetae small, simple-pointed, in subsequent segments gradually enlarging; V−VIII ventral chaetae 1−2, very long, stout, with bluntly bifid tip; preclitellar dorsal chaetae smaller, bluntly bifid; tail region smaller chaetae, upper tooth length ≥ lower; L = 30 mm (Fig. 12.20(63−69)) ..... *Limnodrilus nitens* (Semernoy, 1982) [Lake Baikal]

Oligochaeta: Tubificidae: *Tasserkidrilus*: Species (Lake Baikal)

1 Hair chaetae in dorsal bundles 2

1′ No hair chaetae 3

2(1) Penis sheaths funicular, with sharp distal appendage and lateral opening; spermathecal ampulla bipartite; anterior dorsal bundles 1−2 hair chaetae and 2−4 pectinate chaetae with slightly longer upper tooth and 2−3 intermediate denticles; posteriorly one hair and two bifid chaetae per bundle; ventral chaetae anteriorly 3−4, posteriorly 2−3, with slightly longer upper tooth; L = 20 mm (Fig. 12.21(7−10)) ..... *Tasserkidrilus baicalensis* (Semernoy, 1982) [Lake Baikal and Angara River in Siberia]

2′ Penis sheaths short, tubular, distal opening oblique, proximal collar wide; spermathecal ampulla simple; dorsal hair chaetae 1−3 per bundle; forebody dorsal pectinate chaetae 3−4, posteriorly 1−2, with longer upper tooth and obscure intermediate denticles; ventral chaetae 2−5, upper tooth length four times lower; L = 17−20 mm; abyssal (Fig. 12.21(11−13)) ..... *Tasserkidrilus taediosus* (Čekanovskaja, 1975) [Lake Baikal]

3(1) All chaetae bifid, without intermediate denticles 4

3′ All dorsal chaetae pectinate, teeth equal with long intermediate denticles; forebody 4−7 per bundle, posteriorly three; ventral chaetae 4−6 and three, respectively, with slightly longer upper tooth; penis sheaths tubular, with distal end symmetrical, wide proximal collar occupying a penial sac internal fold; L = 15 mm; Proval Bay (Fig. 12.21(1−6)) ..... *Tasserkidrilus penicraspedifer* (Semernoy, 1982) [Lake Baikal]

4(3) Penis sheaths funicular 5

4′ Penis sheaths long tubular. Spermathecal ampullae bipartite 6

5(4) Penis sheaths with sharp, often bent and finely barbed distal appendage and lateral opening; spermathecal ampullae simple; chaetae 4−5 per bundle, with equally long teeth or slightly longer upper tooth; L = 15 mm ..... *Tasserkidrilus variabilis* (Semernoy, 1982) [Lake Baikal and Angara River in Siberia]

5′ Penis sheaths with slightly oblique opening; spermathecal ampulla bipartite; forebody chaetae 3−5 per bundle, with longer upper tooth; postclitellar bundles 2−3 chaetae with equal teeth; L = 5 mm; sublittoral and abyssal (Fig. 12.21(14−17)) ..... *Tasserkidrilus infundibuliferus* (Isossimov, 1972) [Lake Baikal]

6(4) Penis sheaths proximally dilatated; at least some chaetae with rudimentary teeth 7

6′ Penis sheaths slightly dilated proximally; distal end narrow or slightly dilated, barbed; chaetae bifid with well-developed teeth, upper slightly shorter than lower; L = 8.5−8.8 mm; littoral (Fig. 12.21(18−21)) ..... *Tasserkidrilus mirandus* (Snimschikova, 1982) [Lake Baikal]

7(6) Anteriormost bundle chaetae with reduced, blunt-tipped teeth 8

7′ Preclitellar chaetae enlarged, with long upper and rudimentary lower tooth, 2−3 per bundle; postclitellar chaetae 1−2, with subequal teeth; penis sheaths distally not dilated; L = 7−10 mm; sublittoral (Fig. 12.21(22−25)) ..... *Tasserkidrilus timmi* Akinschina & Snimschikova, 1993 [Lake Baikal]

8(7) Penis sheaths somewhat curved, proximal ends only slightly dilated; chaetae either with rudimentary or developed teeth, equally long or upper tooth slightly longer even in same bundle; chaetae 3−4 in anteriormost and 2−3 in posterior bundles; VI−VIII are five per bundle, longest with well-developed teeth; L = 8−10 mm; littoral ..... *Tasserkidrilus heterodontus* Akinschina & Snimschikova, 1993 [Lake Baikal]

8′ Penis sheaths straight, proximal ends funicular, distal ends slightly dilated; preclitellar bundles chaetae with variable length teeth (and rate) in same bundle but increasing from II to VIII; II−III chaetae four per bundle, IV−V with 4−6, VIII−X with five; L ≥ 2 mm; littoral ..... *Tasserkidrilus rectitubifer* Akinschina & Snimschikova, 1993 [Lake Baikal]

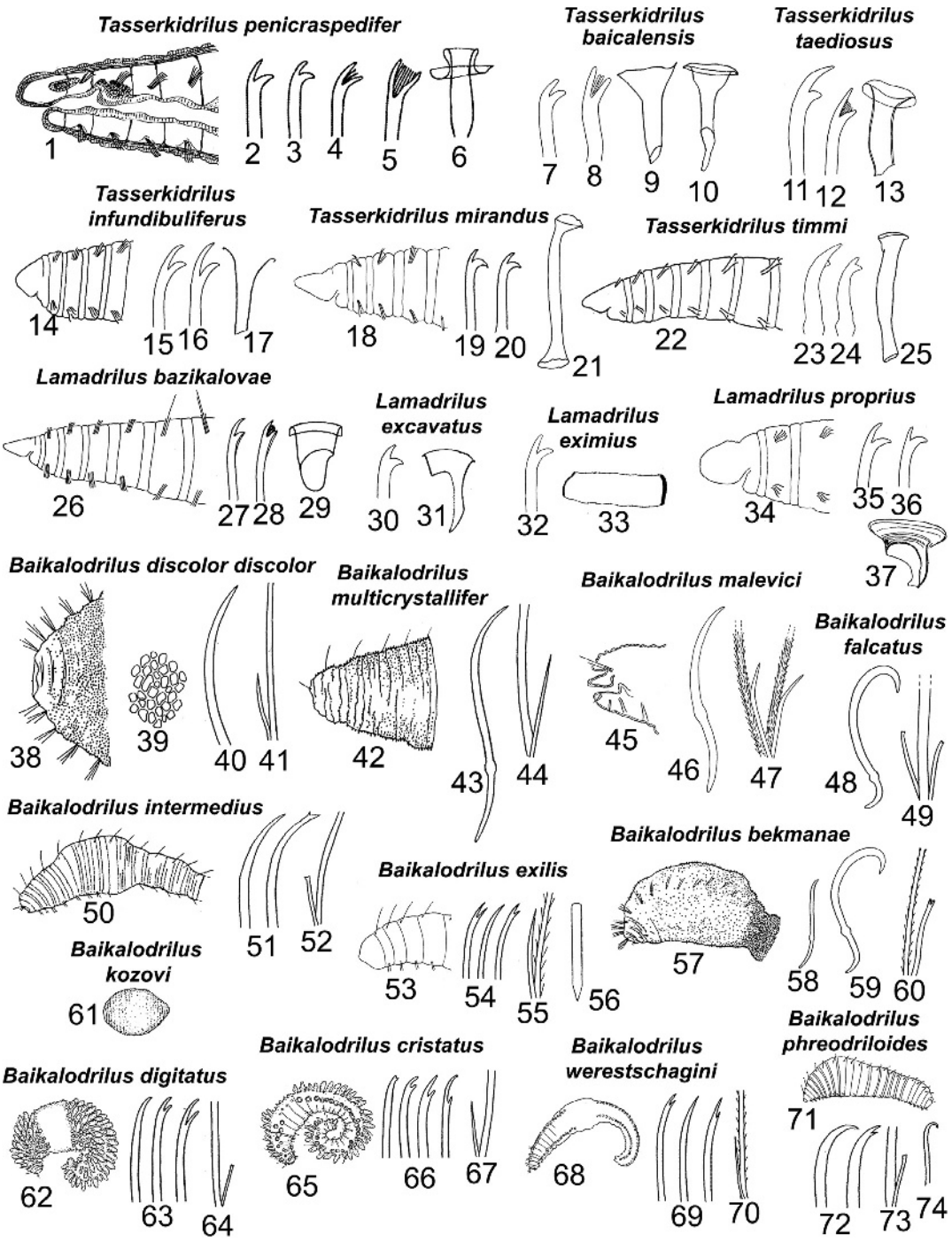


FIGURE 12.21 Tubificidae from Lake Baikal II: (1–6): *Tasserkidrilus penicraspedifer*: (1) anterior end, (2, 3) anterior ventral chaetae, (4, 5) pectinate chaetae, (6) penis sheath; (7–10): *Tasserkidrilus baicalensis*: (7) anterior ventral chaeta, (8) pectinate chaeta, (9, 10) penis sheaths; (11–13): *Tasserkidrilus taediosus*: (11) anterior ventral chaeta, (12) pectinate chaeta, (13) penis sheath; (14–17): *Tasserkidrilus infundibuliferus*: (14) anterior end, (15, 16) anterior chaetae, (17) penis sheath; (18–21): *Tasserkidrilus mirandus*: (18) anterior end, (19, 20) anterior chaetae, (21) penis sheath; (22–25): *Tasserkidrilus timmi*: (22) anterior end, (23) anterior chaeta, (24) posterior chaeta, (25) penis sheath; (26–29): *Lamadrilus bazikalovae*: (26) anterior end, (27) anterior ventral chaeta, (28) pectinate chaeta, (29) penis sheath; (30, 31): *Lamadrilus excavatus*: (30) chaeta, (31) penis sheath; (32, 33): *Lamadrilus eximius*: (32) chaeta, (33) penis sheath; (34–37): *Lamadrilus proprius*: (34) anterior end, (35, 36) chaetae, (37) penis sheath; (38–41): *Baikalodrilus discolor discolor*: (38) anterior end, (39) armor surface, (40) ventral chaeta, (41) dorsal chaetae; (42–44): *Baikalodrilus multicrystallifer*: (42) anterior end, (43) ventral chaeta, (44) dorsal chaetae; (45–47): *Baikalodrilus malevici*: (45) anterior end, (46) ventral chaeta, (47) dorsal chaetae; (48, 49) *Baikalodrilus falcatus*: (48) ventral chaeta, (49) dorsal chaetae; (50–52): *Baikalodrilus intermedius*: (50) forebody, (51) ventral chaetae, (52) dorsal chaetae; (53–56): *Baikalodrilus exilis:* (53) anterior end, (54) ventral chaetae, (55) dorsal chaetae, (56) "crystal" from atrium; (57–60): *Baikalodrilus bekmanae*: (57) forebody, (58) anterior ventral chaeta, (59) posterior ventral chaeta, (60) dorsal chaetae; (61) *Baikalodrilus kozovi*, general view; (62–64): *Baikalodrilus digitatus*: (62) general view of sexually mature specimen with clitellum, (63) ventral chaetae, (64) dorsal chaetae; (65–67): *Baikalodrilus cristatus*: (65) general view of sexually mature specimen with clitellum, (66) ventral chaetae, (67) dorsal chaetae; (68–70): *Baikalodrilus werestschagini*: (68) general view of sexually mature specimen with clitellum, (69) ventral chaetae, (70) hair chaeta; (71–74): *Baikalodrilus phreodriloides*: (71) general view, (72) ventral chaetae, (73) dorsal chaetae, (74) distal end of hair chaeta.

Oligochaeta: Tubificidae: *Lamadrilus*: Species (Lake Baikal)

1 Penis sheaths conical, with distal opening wide, oblique 2

1′ Penis sheaths very short, annular, with asymmetrically thickened wall; chaetae 4–5 per bundle, bifid with longer distal tooth; L = 20 mm; littoral (Fig. 12.21(32, 33)) ..... *Lamadrilus eximius* (Semernoy, 1982) [Lake Baikal]

2(1) No hair chaetae 3

2′ In anteriormost dorsal bundles only 3–5 bifid but from IV–VII 1–2 hair and 3–4 pectinate chaetae with longer upper tooth; anteriormost ventral bundles with 5–7 bifid chaetae, upper tooth as in pectinate chaetae; spermathecal duct long, with well-developed ring musculature; L = 10–12 mm (Fig. 12.21(26–29)) ..... *Lamadrilus bazikalovae* (Čekanovskaja, 1975) [Lake Baikal]

3(2) No pectinate chaetae; body wall not especially thick; chaetae with equal teeth or upper tooth shorter; spermatozeugmata suboval, enclosed in shells of chitin-like material 4

3′ Preclitellar chaetae 5–7, with equal teeth or upper tooth slightly longer, bifid but can be pectinate in dorsal bundles; body wall and dissepiments thick, muscular; penis sheaths with long distal spade-like appendage on one side; spermathecal ducts short; spermatozeugmata without chitin-like shell; littoral (Fig. 12.21(30, 31))) ..... *Lamadrilus excavatus* (Hrabě, 1982) [Lake Baikal]

4(3) Spermathecal ducts long, proximal portion with thicker wall; spermatozeugmata shell with a pore; penis sheath with oblique distal edge; littoral ..... *Lamadrilus penicatus* Semernoy, 2004 [Lake Baikal]

4′ Spermathecal ducts short and wide, with terminal sphincter; spermatozeugmata shell closed; penis sheath with small appendage on one side; profundal (Fig. 12.21(34–37)) ..... *Lamadrilus proprius* Semernoy, 2004 [Lake Baikal]

Oligochaeta: Tubificidae: *Baikalodrilus*: Species (Lake Baikal)

1 Papillae relatively small, sometimes obscure 2

1′ Papillae very long, especially dorsally, comparable in length with chaetae 23

2(1) Dorsal hair chaetae accompanied with bifid or pectinate chaetae 3

2′ Dorsal hair chaetae accompanied with shorter, simple-pointed chaetae 18

3(2) Only 1–2 “crystals” per atrium 4

3′ A cluster of small “crystals” per atrium 22

4(3) Hair chaetae not hooked distally 5

4′ Dorsal bundles with one hair chaeta and one much thinner, slightly sigmoid, aciculate chaeta; hair chaetae distally hooked; aciculate chaetae either blunt or with short teeth; anterior ventral bundles typically with two sigmoid chaetae, one being simple, the other with rudimentary tooth; single simple-pointed chaetae in posterior bundles; body short, plump, foreign particles adhering to intersegmental grooves only; L = 3–4.4 mm; littoral (Fig. 12.21(71–74)) ..... *Baikalodrilus phreodriloides* (Michaelsen, 1905) [Lake Baikal]

5(4) Hair chaetae smooth (sometimes fine pilosity visible at very high magnification?) 6

5′ Hair chaetae distinctly pilose or serrate 11

6(5) Hair chaetae accompanied by bifid, not pectinate chaetae 7

6′ Hair chaetae accompanied by pectinate chaetae 10

7(6) Dorsal bifid chaetae with well-developed teeth; body very short, cylindrical or oval 8

7′ Dorsal bifid chaetae with rudimentary teeth; body vermiform 9

8(7) Anterior ventral bundles with one simple and one bifid chaeta with teeth equal or upper tooth shorter; dorsal bundles with one hair and one bifid chaeta; no epidermal papillae, body covered with thin layer of adhering particles; L = 2–2.5 mm; littoral and sublittoral ..... *Baikalodrilus parilis* Semernoy, 2004 [Lake Baikal]

8′ All ventral chaetae bifid, two in anterior and single in posterior bundles; dorsal bundles with one hair and one bifid chaeta; transverse rows of small epidermal papillae; body covered with thin layer of secretion and adhering foreign particles; L = 1.2 mm; littoral and sublittoral (Fig. 12.21(61)) ..... *Baikalodrilus kozovi* (Hrabě, 1969) [Lake Baikal]

9(7) Dorsal shorter chaetae bifid with rudimentary teeth, with two similar to hair chaetae; ventral chaetae single per bundle, very large and arcuate with strongly proximal nodulus; epidermal papillae small; L = 7.5 mm; littoral (Fig. 12.21(48, 49)) ..... *Baikalodrilus falcatus* (Snimschikova, 1982)
[Lake Baikal]

9′ Dorsal shorter chaetae either bifid with rudimentary teeth or simple, very small; hair chaetae smooth (or very finely pilose?), both one per bundle; ventral chaetae mucronate, bifid with upper tooth rudimentary, or simple-pointed, two in anterior and single in posterior bundles; no epidermal papillae, fine adhering particles in intersegmental grooves only; L = 2.5−4 mm; profundal (Fig. 12.21(50−52)) ..... *Baikalodrilus intermedius* (Snimschikova, 1991)
[Lake Baikal]

10(6) Anterior ventral bundles with one simple and one bifid chaeta with much longer upper tooth; dorsal bundles of one hair and one pectinate chaeta; no epidermal papillae but thin armor of fine adhering particles; L = 3−4 mm; littoral ..... *Baikalodrilus vicinus* Semernoy, 2004

10′ Ventral bundles with only bifid chaetae, lower tooth slightly longer; anterior bundles 3−4 per bundle, posterior 1−2; anterior dorsal bundles with 2−4 hair and 2−4 pectinate chaetae, the latter with fine membrane or intermediate denticle between equal, thin teeth; epidermal papillae small but dense, in tail region forming transverse rings; L = 40 mm; all zones ..... *Baikalodrilus inflatus* (Michaelsen, 1901)
[Lake Baikal and dubious records from the vicinity]

11(5) Dorsal shorter chaetae pectinate 12

11′ Anterior dorsal bundles four bifid chaetae with long teeth, and 2−3 hair chaetae; posterior bundles only single hair chaetae; anterior ventral chaetae 3−4 per bundle, decreasing to one in posterior segments; simple-pointed and bifid chaetae with shorter upper tooth in same bundle; epidermal papillae small and forming transverse rows in forebody, larger and irregularly dispersed posteriorly; L = 8−8.5 mm; littoral ..... *Baikalodrilus bifidus* Snimschikova, 1989
[Lake Baikal]

12(11) Pectinate chaetae with distinct intermediate denticles 13

12′ Pectinate chaetae with short teeth and thin, obscure, connecting membrane, four per bundle in anterior segments, with 4−5 short hair chaetae; both kinds decreasing to one in tail region; ventral chaetae simple-pointed and bifid with variable teeth length in same bundle; II with 6−7 per bundle, gradually decreasing to one posteriorly; epidermal papillae arranged in transverse rows, small in forebody, larger and denser in mid- and hindbody; body 3.5−3.8 mm in diameter; L = 32−35 mm; littoral and sublittoral ..... *Baikalodrilus crassus* Snimschikova, 1989
[Lake Baikal]

13(12) Pectinate chaetae teeth short 14

13′ Anterior bundles 2−3 serrate hair chaetae and 2−3 pectinate chaetae; postclitellar bundles one hair and one aciculate chaeta; pectinate chaetae teeth and intermediate denticles relatively long; II ventral chaetae three, in next preclitellar segments two, in postclitellar segments one per bundle; simple-pointed and bifid chaetae with equal teeth or rudimentary upper in same bundle; epidermal papillae well developed, armor thick, ringed; L = 24 mm ..... *Baikalodrilus paradoxus* (Snimschikova, 1984)
[Lake Baikal]

14(13) II ventral chaetae with rudimentary teeth; no epidermal papillae 15

14′ II ventral chaetae simple-pointed (upper tooth can occur in posterior segments, as well as simple-pointed chaetae) 16

15(14) Pectinate chaetae 2−3, with two intermediate denticles; hair chaetae 2−3; anteriormost bundles with two ventral chaetae, bifid with varying teeth (equal, or upper shorter); from VII−VIII single and simple-pointed; adhering particles armor thin, transparent and transversely striped; L = 14−16 mm; littoral ..... *Baikalodrilus scaphoideus* Snimschikova, 1989
[Lake Baikal]

15′ Pectinate chaetae two per bundle, with a single, thick intermediate denticle; hair chaetae two, serrate; preclitellar ventral bundles with two chaetae, one simple-pointed, the other bifid; II and postclitellar bundles with bifids bearing rudimentary teeth; III−X with teeth equal or upper shorter; armor thin, with fine transverse folds; L ≥ 6.5 mm; littoral ..... *Baikalodrilus undatus* Snimschikova, 1989
[Lake Baikal]

16(14) All ventral chaetae simple-pointed 17

16′ II ventral bundles with two simple-pointed and one bifid chaeta with longer upper tooth; other preclitellar bundles one simple-pointed and one bifid chaeta with equal teeth; postclitellar bundles one simple-pointed and one bifid chaeta with short, blunt teeth; II dorsal bundles with three hair chaetae and two bifid or pectinate chaetae with three intermediate denticles; chaetal number decreasing posteriorly; armor thick, papillae large, in transverse rows in forebody but irregularly distributed on postclitellar segments; L = 14 mm; littoral ..... *Baikalodrilus medianus* Snimschikova, 1991
[Lake Baikal]

17(16) All ventral chaetae mucronate, two (3) in preclitellar and single in postclitellar bundles; dorsal bundles with 2−5 hair chaetae and 3−6 thinner pectinate chaetae with blunt teeth and obscure intermediate denticles; papillae ovoid, sparsely distributed; L = 24 mm; sublittoral ..... *Baikalodrilus discolor brevipectinatus* Snimschikova, 1989
[Lake Baikal]

17′ II–IV(V) ventral chaetae small and mucronate, two (3) per bundle, in several following segments single; ventral chaetae lacking in midbody, beginning again in XX–XXV; then single, large and arcuate, with strongly proximal nodulus; II–IV dorsal bundles 4–5 hair chaetae and 5–6 pectinate chaetae with equal teeth and obscure intermediate denticles; posteriorly gradually decreasing to two hair and two pectinate chaetae; body short, preclitellar portion inflated; papillae well developed, irregularly distributed, most dense and largest in midbody; L = 8–10 mm; littoral (Fig. 12.21(57–60)) ..... *Baikalodrilus bekmanae* (Snimschikova, 1984) [Lake Baikal]

18(2) Hair chaetae pilose 19

18′ Hair chaetae smooth 21

19(18) Anterior ventral chaetae two, one simple-pointed, the other bifid with longer upper tooth; hindbody ventral chaetae single but larger; dorsal bundles with one hair chaeta and one simple-pointed aciculate chaeta..... 20

19′ Ventral chaetae mucronate with proximal nodulus, becoming larger posteriorly; two per bundle in anterior segments and single in post-clitellar segments; dorsal bundles 5–6 hair chaetae and 3–4 thin, slightly sigmoid, simple-pointed aciculate chaetae; body segments extended; papillae well developed but sparse; L = 12–25 mm (Fig. 12.21(45–47)) ..... *Baikalodrilus malevici* (Čekanovskaja, 1975) [Lake Baikal]

20(19) Body terete; no epidermal papillae, armor thin; L = 2.3 mm (Fig. 12.21(53–56)) ..... *Baikalodrilus exilis* (Snimschikova, 1982) [Lake Baikal]

20′ Body square in cross-section; chaetal bundles on long, light papillae; epidermal papillae long, agglomerated into continuous thick armor; L = 3.1–3.5 mm (Fig. 12.21(68–70)) ..... *Baikalodrilus wereststchagini* (Michaelsen, 1933) [Lake Baikal]

21(18) Dorsal short chaetae very thin and acute, two per bundle; hair chaetae 2–5 in anterior and two in posterior bundles; II ventral chaetae three, following segments two per bundle, mucronate, considerably larger in the posterior segments; papillae smaller and sparse on anteriormost segments and ventrally, forming a continuous armor on clitellum dorsally, covered with secretion clumps in postclitellar region; body color in mature individuals dark brown in forebody to beige in clitellum and orange in several portions of postclitellar region; L = 28–30 mm (Fig. 12.21(38–41)) ..... *Baikalodrilus discolor discolor* (Snimschikova, 1984) [Lake Baikal]

21 Dorsal short chaetae thin and blunt, two per bundle; hair chaetae 2–3; anterior bundles ventral chaetae 2–3, posterior one, mucronate; papillae well developed, denser in postclitellar portion, forming a thick armor; L = 20 mm; profundal ..... *Baikalodrilus discolor acinacifer* Snimschikova, 1989 [Lake Baikal]

22(3) A cluster of "crystals" in atrial duct; anterior dorsal bundles with 2–4 almost smooth hair chaetae and two simple-pointed aciculate chaetae; posterior bundles one hair and one aciculate chaeta; ventral chaetae mucronate, II usually two, III–V up to four, posterior segments one; papillae well developed, in anterior segments sparse, in midbody forming transverse rows, and in tail region continuous; L = 14–18 mm; sublittoral (Fig. 12.21(42–44)) ..... *Baikalodrilus multicrystallifer* Snimschikova, 1989 [Lake Baikal]

22′ A cluster of "crystals" attached externally to atrial duct (an artifact?); dorsal bundles with two distinctly pilose hair chaetae and three very small, simple-pointed aciculate chaetae; ventral chaetae two per bundle, mucronate; papillae small; L = 11.5 mm; littoral ..... *Baikalodrilus solitarius* (Snimschikova, 1982) [Lake Baikal]

23(1) Dorsal papillae digitiform, arranged into transverse rows 24

23′ Dorsal papillae suboval, irregularly placed; ventral bundles one simple-pointed and one bifid chaeta, the latter with long, subparallel teeth, the lower much shorter; dorsal bundles with one hair and one thin, sharp aciculate chaeta; L = 3–4 mm; littoral ..... *Baikalodrilus dividus* Semernoy, 2004 [Lake Baikal]

24(23) Papillae gradually increasing in length from body ventral to dorsal side; ventral bundles one simple-pointed and one bifid chaetae with longer upper tooth; dorsal bundles one hair and one very thin aciculate chaeta with reduced teeth; L = 3–3.5 mm; profundal (Fig. 12.21(62–64)) ..... *Baikalodrilus digitatus* Holmquist, 1979 [Lake Baikal]

24′ Body dorsally with a longitudinal ridge formed by the longest papillae; anterior ventral bundles simple-pointed and bifid chaetae, the latter with short teeth; posterior bundles only single bifids with longer upper tooth; dorsal bundles one hair and one very thin aciculate chaeta with simple sharp tip; L = 3 mm (Fig. 12.21(65–67)) .....*Baikalodrilus cristatus* (Snimschikova, 1982) [Lake Baikal]

Oligochaeta: Tubificida: Phreodrilidae: Genera

1 Hair and supporting chaetae present in dorsal bundles 2

1′ All chaetae bifid, with smaller upper tooth; dorsal chaetae smaller and single (2), ventrally larger and paired but absent in XII; two modified spermathecal chaetae per bundle in XIII: one distally hollow, straight, with bent proximal tip in a glandular sac, the other chaeta smaller as a simple rod; L ≥ 3 mm (Fig. 12.22(1–4)) ..... *Astacopsidrilus ryuteki* Martin & Ohtaka, 2008 [Japan: Lake Biwa]

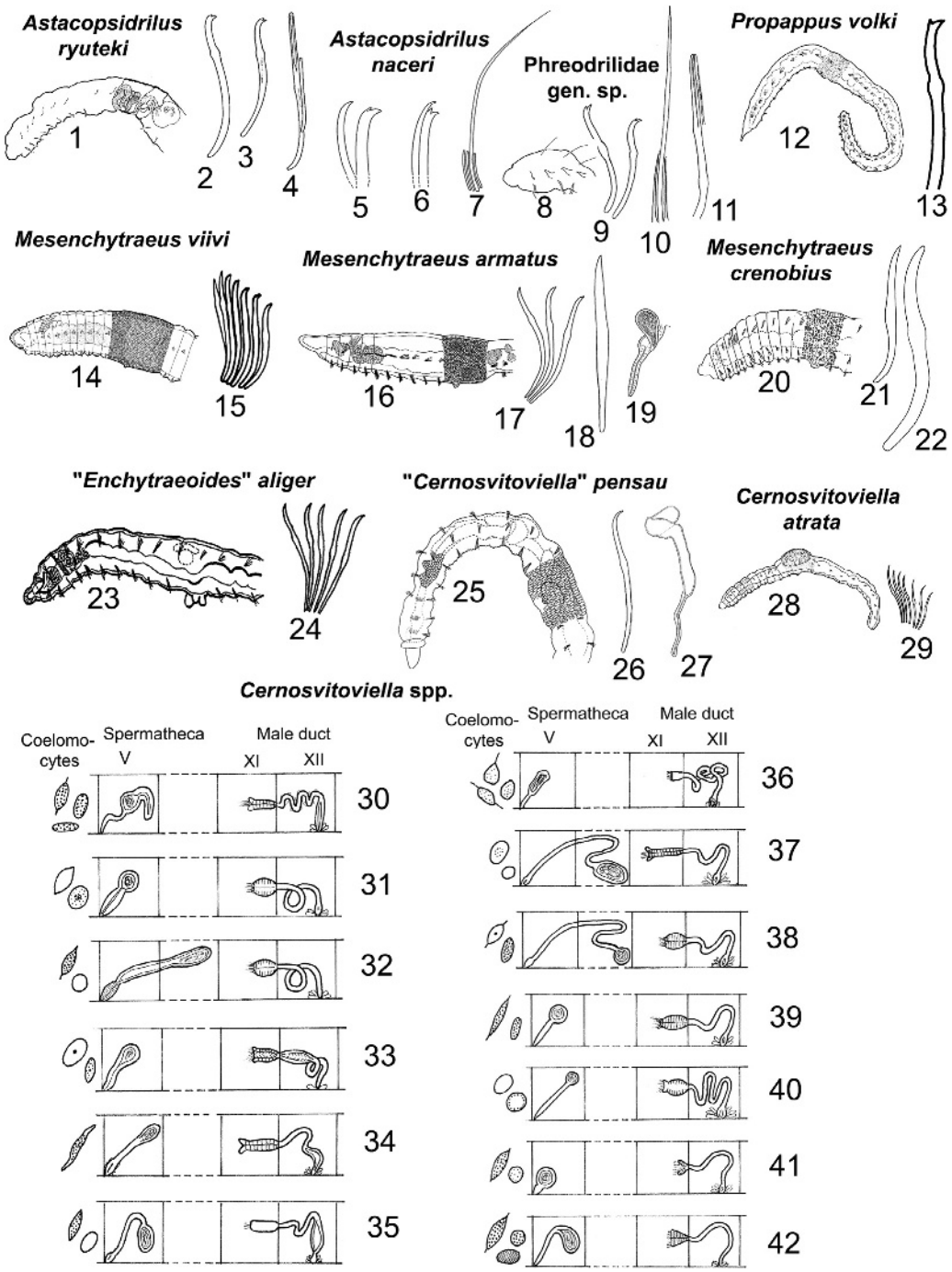


FIGURE 12.22 Phreodrilidae, Propappidae and Enchytraeidae: (1–4): *Astacopsidrilus ryuteki*: (1) forebody of sexually mature specimen with clitellum, (2) ventral chaeta, (3) dorsal chaeta, (4) spermathecal chaetae; (5–7): *Astacopsidrilus naceri*: (5) anterior ventral chaetae, (6) posterior ventral chaetae, (7) dorsal chaetae; (8–11): Phreodrilidae gen. sp. from north Ireland; (8) anterior end, (9) ventral chaetae, (10) dorsal chaetae with support chaetae, (11) spermathecal chaeta; (12, 13): *Propappus volki*: (12) general view of sexually mature specimen with clitellum, (13) chaeta; (14, 15) *Mesenchytraeus viivi*: (14) forebody of sexually mature specimen with clitellum, (15) chaetae; (16–19): *Mesenchytraeus armatus*: (16) forebody of sexually mature specimen with clitellum, (17) ordinary chaetae, (18) dorsal giant chaeta, (19) spermathecal; (20–22): *Mesenchytraeus crenobius*: (20) forebody of sexually mature specimen with clitellum, (21) ordinary chaetae, (22) ventral giant chaeta; (23, 24) "*Enchytraeoides*" *aliger:* (23) forebody of sexually mature specimen with sexual flaps, (24) chaetae; (25–27): "*Cernosvitoviella*" *pensau*: (25) forebody of sexually mature specimen with clitellum, (26) chaeta, (27) spermathecal; (28, 29): *Cernosvitoviella atrata*: (28) general view of sexually mature specimen with clitellum, (29) chaetae; (30–42): scheme of some anatomical characters in *Cernosvitoviella* spp.: (30) *C. immota*, (31) *C. carpatica*, (32) *C. tatrensis*, (33) *C. crassoducta*, (34) *C. aggtelekensis*, (35) *C. parviseta*, (36) *C. longiducta*, (37) *C. palustris*, (38) *C. sphaerotheca*, (39) *C. minor*, (40) *C. tridentina*, (41) *C. microtheca*, (42) *C. atrata*.

2(1) Hair chaetae one (2) in III, in subsequent segments 7−9 per bundle, each flanked by 2−4 blunt supporting chaetae hidden inside body wall; each ventral bundle with one simple-pointed and one bifid chaeta, the latter with shorter upper tooth; no chaetae in XII; no modified genital chaetae; length ≥9 mm; groundwater (Fig. 12.22(5−7)) ..... *Astacopsidrilus naceri* Giani & Martin, 1995 [Morocco]

2′ Hair chaetae 1−2 beginning in III, each flanked by two short, straight needle chaetae with flared distal end; ventral chaetae two, stout, bifid with shorter upper tooth, lacking in XII; spermathecal chaetae two in XIII, inequal, the larger slightly sigmoid and with distal half hollow, the smaller baciliform, with flared end; L ≥ 3 mm (Fig. 12.22(8−11)) ..... *Astacopsidrilus* sp./*Insulodrilus* sp., incertae sedis [Northern Ireland (probably introduced)]

Oligochaeta: Enchytraeida: Families

1 Chaetae bifid, mostly three per bundle, upper tooth shorter; testes in XI, ovaria in XIII; spermathecal pores in IV ..... **Propappidae**, one genus: ***Propappus*** **[p. 445]**

1′ Chaetae simple-pointed, of variable number, seldom lacking; testes usually in XI, ovaria in XII (seldom both shifted forward); spermathecal pores in 3−4 ..... **Enchytraeidae [p. 445]**

Oligochaeta: Enchytraeida: Propappidae: *Propappus*: Species

1 No proboscis 2

1′ Prostomium with short proboscis; chaetae three (4) per bundle, each with two large glands; L = 4−12 mm (Fig. 12.22(12, 13)) ..... *Propappus volki* Michaelsen, 1916 [Palaearctic]

2(1) Chaetae (2) three per bundle; VIII with esophagus widening into midgut; spermathecal ampullae reaching VI; male pores indistinct; L = 4−5 mm. ..... *Propappus glandulosus* Michaelsen, 1905 [Russia: Lake Baikal, Angara and Enisej River in Siberia]

2′ Chaetae (1, 2) three (4, 6) per bundle; XIII with esophagus widening into midgut; spermathecal ampullae cylindrical, mostly in V; male pores on coniform papillae, often protracted as a short penis; L = 4−12 mm. ..... *Propappus arhynchotus* Sokolskaja, 1972 [Russia]

Oligochaeta: Enchytraeida: Enchytraeidae: Genera

A large number of enchytraeids are terrestrial but can accidentally occur in water bodies, besides the mostly aquatic and amphibious species keyed below.

1 Chaetae sigmoid, arranged in unilateral flabelliform bundles 2

1′ Chaetae straight or irregularly bent, arranged in symmetrical bundles, seldom completely lacking 9

2(1) Chaetae with nodulus 3

2′ Chaetae without nodulus 5

3(2) Length a few millimeters; sexually mature individuals with one, sometimes two, mature eggs occupying only clitellar region; spermathecae always free 4

3′ Length usually about 10 mm or more (with some exceptions); sexually mature individuals with egg sac bearing numerous eggs extending into several segments beyond clitellum; spermathecae usually entally connected to esophagus entally; male duct distal end with complicated penial apparatus consisting of epithelial and muscular tissue and prostate glands ..... ***Mesenchytraeus*** **[p. 446]**

4(3) Body wall epithelium with thin ventrolateral folds, often consisting of 2−3 lobes (but sometimes lacking) in XII laterad of male pores; chaetae sigmoid with nodulus, dorsal bundles with 4−6 and ventral with 5−7 (8) (10?); male duct distally forming a muscular penial bulb covered with high prostate cells; spermathecae consisting of sacculate or tubular ampulla, not connected with esophagus, and of short, clearly separate duct, without diverticula or external glands; L = 2.5−5.5 mm; littoral and supralittoral (Fig. 12.22(23, 24)) ..... "*Enchytraeoides*" *aliger* Michaelsen & Vereščagin, 1930, incertae sedis [Russia: Lake Baikal littoral, maybe a species complex (Timm, 2003)]

4′ Genital segments without ventrolateral epithelial folds; male duct distally simple or slightly dilated, with small glands around the male pore ..... ***Cernosvitoviella*** **[p. 448]**

5(2) At least some anterior bundles with more than three chaetae 6

5′ Chaetae three (rarely two or four) per bundle; asexual reproduction by fragmentation, regenerating anterior or posterior ends often present; sexually mature individuals clitellum with male pore often shifted forward into VIII, IX, X, or XI ..... ***Chamaedrilus*** **[p. 450]**

6(5) No large branching seminal vesicles in X–XI 7

6′ X and XI, sometimes even up to IX or VIII with developing spermatozoa enclosed in numerous sperm vesicle branches attached ventrally to body wall; usually red when alive, due to hemoglobin ..... ***Lumbricillus*** [in part; **p. 450**]

7(6) No esophageal or intestinal appendages 8

7′ Esophagus in IV with four small, spongiform diverticula; 4/5–6/7 with three pairs of pharyngeal glands, without dorsal junctions but with ventral lobes in IV and V; spermathecae consisting of fusiform ampulla and 2.5–3 times longer ectal duct, with a hyaline gland at pore; both ental ducts unite before communication with esophagus; male funnels 2–2.5 times longer than wide, curved, with collar as wide; chaetae strongly sigmoid, (2) 3–6 (7, 8) per bundle; L = 9.5–21 mm; terrestrial and amphibious ..... *Bryodrilus ehlersi* Ude, 1892
[Holarctic]

8(7) Spermathecae V with small suboval ampulla, attached to esophagus with a thin tissue strand, ectal duct long, bare, sometimes with small gland at ectal end; sperm arranged in circles in spermathecal ampullae; male funnels short, cylindrical, length three times width, with collar slightly narrower, indistinct; 4/5–6/7 with three pairs of small pharyngeal glands that can be dorsally narrowly connected; chaetae 2–5, slightly sigmoid in lateral view but almost straight otherwise; L = 3–8 mm; terrestrial, amphibious (Fig. 12.23(12–14)) ..... *Globulidrilus riparius* (Bretscher, 1899, emend. Černosvitov, 1928)
[Holarctic]

8′ Spermathecae attached to esophagus, with small suboval ampulla and a small diverticulum; ectal duct long, thin and bare; spermathecal pores with large glands; three pairs of pharyngeal glands; no intestinal appendages; chaetae slightly sigmoid, stout and obtuse, 4–8 per bundle; dorsal blood vessel beginning in VIII; male funnels large, cylindrical, with narrower collar; length 9–15 mm ..... "*Henlea*" *pertoserica* Popčenko, 1988, incertae sedis
[Russia: Lake Pertozero in Karelia]

9(1) No multibranched sperm vesicles in X–XI 10

9′ Developing spermatozoa enclosed in multibranched sperm vesicles (testis sacs) attached to body wall 10/11 and extending into X and XI; male funnels tubular, ≤15 times as long as wide, three times longer than body diameter, collar short and narrow; spermathecae clavate, with ectal duct conical and thick-walled, narrow ectal end surrounded by crown of high glands, ental end wide as suboval ampulla; in ampulla 1–4 spherical spermatozoa bundles; three pairs of pharyngeal glands united dorsally; chaetae in forebody three (4), posteriorly with two per bundle, straight but with a proximal hook, distally narrowing, acute; L = 5–17 mm; brackish and fresh water. ..... *Lumbricillus arenarius* (Michaelsen, 1889)
[Russia: Lake Kurilskoe on Kamchatka Peninsula]

10(9) Chaetae more than two at least in some bundles 11

10′ Chaetae in all bundles either paired, single, or lacking ..... ***Enchytraeus/Marionina*** [in part; **p. 451**]

11(10) Chaetae either straight or slightly bent, arranged in symmetrical flabelliform bundles, more than three at least in some bundles 12

11′ Chaetae in bundles of 2–3 ..... ***Enchytraeus/Marionina*** [in part; **p. 451**]

12(11) VIII without intestinal diverticula 13

12′ Intestine beginning in IX, with diverticula in VIII beside esophagus; chaetae subequally long and thick, in flabelliform bundles ..... ***Henlea*** [in part; **p. 453**]

13(12) Middle chaetae in each flabelliform bundle shorter than the outer 14

13′ Chaetae in bundles subequally long ..... ***Enchytraeus/Marionina*** [in part; **p. 451**]

14(13) Chaetae aciculate, distally tapering, 3–6 in dorsal bundles, 4–8 in ventral bundles; the medium chaetae in each bundle shorter but distal ends aligning with the rest; no intestinal appendages ..... ***Henlea*** [in part; **p. 453**]

14′ Chaetae mostly obtuse, inner ones much shorter and thinner, distal ends lying lower; spermathecae often with diverticula; coelomocytes abundant, of two kinds; terrestrial worms with relatively thick body wall, often accidentally in water (Fig. 12.23(20, 21)) ..... *Fridericia* (many species)

Oligochaeta: Enchytraeida: Enchytraeidae: *Mesenchytraeus*: Species

1 Single giant chaetae, longer and thicker than the rest, present in some anterior bundles 2

1′ All chaetae uniform, no giant chaetae present 5

2(1) Giant chaetae present in ventral bundles 3

2′ In some anterior dorsal bundles (most often V–VII or V–VIII) giant chaetae 1–2; 2–12 smaller chaetae in other bundles; spermathecae with thin duct, small ampulla and with one, sometimes two diverticula containing sperm; L = 10–17 mm; amphibious (Fig. 12.22(16–19)) ..... *Mesenchytraeus armatus* (Levinsen, 1884)
[Holarctic]

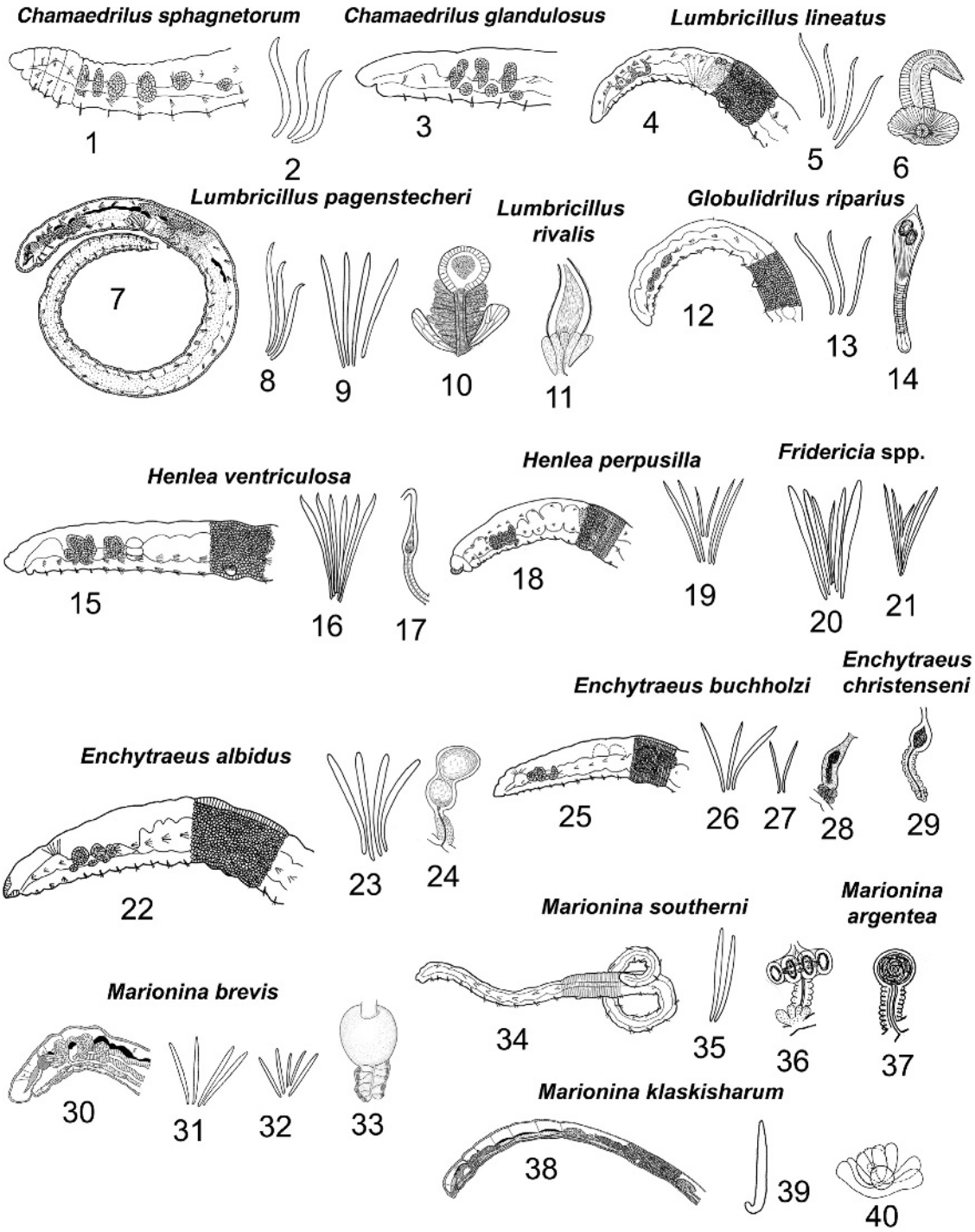


FIGURE 12.23 Enchytraeidae: (1, 2) *Chamaedrilus sphagnetorum*: (1) anterior end, (2) chaetae; (3) *Chamaedrilus glandulosus*, anterior end; (4–6): *Lumbricillus lineatus*: (4) forebody of sexually mature specimen with clitellum, (5) chaetae, (6) spermatheca; (7–10): *Lumbricillus pagenstecheri*: (7) general view of sexually mature specimen with clitellum, (8, 9) chaetae, (10) spermatheca; (11) *Lumbricillus rivalis*, spermatheca; (12–14): *Globulidrilus riparius*: (12) forebody of sexually mature specimen with clitellum, (13) chaetae, (14) spermatheca; (15–17): *Henlea ventriculosa*: (15) forebody of sexually mature specimen with clitellum, (16) chaetae, (17) spermatheca; (18, 19) *Henlea perpusilla*: (18) forebody of sexually mature specimen with clitellum, (19) chaetae; (20, 21) most typical chaetae of *Fridericia* spp.; (22–24): *Enchytraeus albidus*: (22) forebody of sexually mature specimen with clitellum, (23) chaetae, (24) spermatheca; (25–28): *Enchytraeus buchholzi*: (25) forebody of sexually mature specimen with clitellum, (26) anterior ventral chaetae, (27) posterior chaetae, (28) spermatheca; (29) *Enchytraeus christenseni*, spermatheca; (30–33): *Marionina brevis*: (30) anterior end, (31) anterior ventral chaetae, (32) posterior chaetae, (33) spermatheca; (34–36): *Marionina southerni*: (34) general view of sexually mature specimen with clitellum, (35) chaetae, (36) spermatheca; (37) *Marionina argentea*, spermatheca: (38–40): *Marionina klaskisharum*: (38) forebody of sexually mature specimen with clitellum, (39) chaeta, (40) spermathecal pore with glands.

3(2) Giant ventral chaetae present in three segments 4

3′ VI and VII ventral bundles with single giant chaetae, 2−6 smaller chaetae in other bundles; spermathecae with very long, tubular ampullae joining esophagus in IX or X, ectal portion with paired diverticula; L = 10−17 mm; streams. ..... *Mesenchytraeus tetrapodus* Timm, 1978
[Russia: Kola Peninsula]

4(3) V−VII ventral bundles each a single giant chaetae, other ventral bundles 5−7 and dorsal 2−3 smaller chaetae; L = 8−10 mm; amphibious(?) ..... *Mesenchytraeus monochaetus* Bretscher, 1900
[Switzerland: Lake Katzensee]

4′ VI−VIII ventral bundles with giant chaetae 1−3, the largest in VI; anteriodorsal bundle smaller chaetae 2−4, posterior bundles 2−5 (usually 3), and ventral bundles (3) 4−6; spermathecae occupying V–VI and joining esophagus ventrally, with duct wall thick, ampullae ental end with two diverticula containing sperm; L = 8−15.5 mm; springs (Fig. 12.22(20−22)) ..... *Mesenchytraeus crenobius* Timm, 1994
[southeastern Russia]

5(1) Body white or yellowish 6

5′ Body color reddish-brown due to hemoglobin, yellow or brown coelomocytes and chloragogen cells; chaetae 2−5 per bundle; spermathecae tubular and very long, extending to IX–X or further, but not connecting with esophagus; L = 12−15 mm; amphibious. ..... *Mesenchytraeus sanguineus* Nielsen & Christensen, 1959
[western Europe]

6(5) Spermathecae with none to two diverticula 7

6′ Spermathecae occupying V–VI, pyriform ectal duct with walls thick-walled, and ampulla thin-walled, containing sperm; at least six small diverticula, containing sperm, surrounding ampulla ental end; chaetae anteriormost bundles 2−3 and 3−5 elsewhere; L = 5−12.5 mm; springs ..... *Mesenchytraeus vshivkovae* Timm, 1994
[southeastern Russia]

7(6) Spermathecae with 1−2 diverticula 8

7′ Spermathecae without diverticula 9

8(7) Spermathecae ampulla short, cylindrical, 1−2 cylindrical diverticula; ectal duct narrow, with small glands at ectal pore; chaetae anteriodorsal bundles four, posterior bundles 5−8, and ventral bundles 6−9 (10); L = 10−14 mm; lakes (Fig. 12.22(14, 15)) ..... *Mesenchytraeus viivi* Timm, 1978
[Russia: Kola Peninsula]

8′ Spermathecae short, tubular, with a large reniform diverticulum attached to the junction of ampulla and ectal duct; chaetae anterior bundles 4−7 (8, 9) and posterior 2−5; L = 45−6 mm (unusually small) ..... *Mesenchytraeus kuril* Healy & Timm, 2000
[Russia: Lake Kurilskoe on Kamchatka Peninsula]

9(7) Spermathecal ampulla and duct wall smooth, can extend posteriorly 10

9′ Spermathecae small, limited to V, sacciform ampulla elongate, walls thin, sometimes rugose, gradually transiting into rather loose ectal duct; chaetae dorsal bundles 4−5, ventral bundles 4−6; L = 9−15 mm; amphibious. ..... *Mesenchytraeus pelicensis* Issel, 1905
[western Palaearctic]

10(9) Chaetae not abruptly thinner distally 11

10′ Chaetae in forebody 4−6, posteriorly 2−4; chaetae abruptly thinner distally; spermathecae with long sacculate ampullae reaching to IX(X) and gradually transitioning into long ducts; L = 11−15 mm; amphibious. ..... *Mesenchytraeus lusitanicus* Collado, Martínez-Ansemil & Giani, 1993
[Portugal, Spain]

11(10) Spermathecal ampulla suboval or elongate, distal end abruptly separated from the narrower, long duct; spermathecae limited to V; chaetae dorsal bundles 3−6, ventral bundles 4−6; L = 10−20 mm; amphibious ..... *Mesenchytraeus bungei* Michaelsen, 1901
[Russia: Lake Baikal]

11′ Spermathecal duct long and narrow, tubular ampulla usually reaching X; male ducts with funnel oval, vas deferens long and coiled, penial bulb muscular; XII–XIII with numerous eggs; chaetae 5−8 per bundle; L = 5−5.5 mm; streams (Fig. 12.22(25−27)) ..... "*Cernosvitoviella*" *pensau* Timm, 1994 incertae sedis
[southeastern Russia]

Oligochaeta: Enchytraeida: Enchytraeidae: *Cernosvitoviella*: Species

1 No anterior sperm sac; spermathecal ampulla spherical, oval or tubular 2

1′ Unpaired sperm sac reaching forwards as far as VIII; spermathecal duct narrow and slightly shorter than ampulla; ampulla dilated, ectal end containing spermatozoa arranged in rings, ental portion with narrow lumen, walls usually thick; male funnels cylindrical, twice as long as wide, with collar same width; vasa deferentia distal third slightly dilated; coelomocytes fusiform or oval, granulate; dorsal vessel originating in XIII or XIV, blood colorless; chaetae 2−7; L = 5−7 mm; amphibious, fresh and brackish water (Fig. 12.22(30)) ..... *Cernosvitoviella immota* (Knöllner, 1935)
[western Palaearctic. Nearctic]

2(1) Two pairs of pharyngeal glands 3

2′ Pharyngeal gland primary and secondary (ventral) lobes in three pairs, at 4/5–6/7; spermathecal ampulla clearly defined, thin-walled, spherical or oval; duct 2−3 times longer, straight, walls thick; male funnels length 1.5 times width; vasa deferentia short, stout, inflated distally; coelomocytes oval, some with fine tips, either hyaline or slightly granular; dorsal vessel originating in XIII, blood colorless; chaetae 5–9; L = 3−5 mm; amphibious (Fig. 12.22(31)) ..... *Cernosvitoviella carpatica* Nielsen & Christensen, 1959 [Europe]

3(2) Spermathecal duct much narrower than ampulla, not muscular 4

3′ Spermathecal duct 2−3.5 times shorter than ampulla and very muscular; ampulla tubular, thick, usually reaching VI, often with dilatations containing sperm; male funnels small, cylindrical or ovoid, with narrower collar; vasa deferentia relatively short and thick; coelomocytes abundant, round or oval with thin appendages, more or less granulated; dorsal vessel originating in XIII, blood yellow; chaetae 3−9; L = 5−9 mm; cool freshwater and groundwater (Fig. 12.22(32)) ..... *Cernosvitoviella tatrensis* (Kowalewski, 1917) [Europe]

4(3) Vasa deferentia dilated either in proximal or distal third 5

4′ Vasa deferentia of uniform width, or dilated only distally, like a minute penial bulb 7

5(4) Vasa deferentia dilated in distal third; spermathecae with a long, thin duct; ectal pore with small muscular swelling 6

5′ Vasa deferentia dilated in proximal third, posterior to male funnel; male funnel length 1.5–2 times width; spermathecae with ampulla oval, duct 2–2.5 times longer; coelomocytes broadly fusiform, transparent but some granulated darkly; dorsal vessel beginning in XI–XII, blood faintly yellow; chaetae 4−7; L = 3−4 mm; *Sphagnum* moss (Fig. 12.22(33)) ..... *Cernosvitoviella crassoducta* Dózsa-Farkas, 1990 [Europe]

6(5) Spermathecal ampulla oval, containing sperm, can reach VI; duct thinner, 2.5 times longer, with portion widening, orifice bearing some small glands; male funnel cylindrical, length 2.5–3 times width, with collar as wide or narrower; vas deferens dilated distally but narrowing again at male pore; coelomocytes fusiform, filled with refractive granules; dorsal vessel originating in (XIII?) XIV–XV, blood yellowish or slightly pink; chaetae 2−9; L = 1.5−4 mm; amphibious (Fig. 12.22(34)) ..... *Cernosvitoviella aggtelekensis* Dózsa-Farkas, 1970 [Europe]

6′ Spermathecal ampulla cylindrical, containing irregularly arranged sperm; duct well-defined, 2.5–3 times longer, swelling before ectal pore; male funnel cylindrical, length ~three times width, with collar as wide; vas deferens length 2.5–3 times funnel, strongly dilated at half length but narrowing before male pore; fusiform and oval coelomocytes, the oval less numerous; dorsal vessel originating in XIII or XIV; prostomium with large, scattered cutaneous glands arranged in anteclitellar 4−6 rows and 2−3 posterior rows; chaetae 4−8, very short (15−22 µm); L = 2−5 mm; groundwater (Fig. 12.22(35)) ..... *Cernosvitoviella parviseta* Gadzińska, 1974 [Europe]

7(4) Male funnels cylindrical, or pyriform, with distinct, mostly narrower collar 8

7′ Male funnels funicular, without distinct collar 12

8(7) Spermathecal duct longer than ampulla 9

8′ Spermathecal duct slightly shorter than oval ampulla; male funnels cylindrical, slightly longer than wide, with short collar of the same width; vas deferens long, ending with a small spherical dilatation; coelomocytes oval and spherical, both types sparsely granulated; ventral chaetae in anterior segments 5−6 (7) and 4−6 elsewhere; L = 2.5−3.5 mm; streams and lakes (Fig. 12.22(36)) ..... *Cernosvitoviella longiducta* Dumnicka, 2010 [Italy]

9(8) Spermathecae short, in V; ampulla small, spherical, with sperm arranged in a transverse ring 10

9′ Spermathecae with duct very long, ampulla spherical or oval, usually reaching VIII–X 11

10(9) Spermathecal ducts 1.5–3 times as long as ampulla; male funnels pyriform, length two times width, with funnel narrower; coelomocytes fusiform, granular, most narrow and apically acute, others broadly oval; dorsal vessel originating in XII or XIII, blood colourless or light pink; chaetae 3−8; L = 1.5−2.8 mm; amphibious (Fig. 12.22(39)) ..... *Cernosvitoviella minor* Dózsa-Farkas, 1990 [Europe]

10′ Spermathecal ducts 4−5 times longer than ampulla; male funnels small, cylindrical, with slightly narrower collar; coelomocytes scarce, oval or spherical, either transparent or with granules clustered along their walls; dorsal vessel beginning in XIII; chaetae (4) 5−9; L = 2−3.5 mm; alpine streams (Fig. 12.22(40)) ..... *Cernosvitoviella tridentina* Dumnicka, 2004 [Europe]

11(9) Spermathecae usually reaching VIII; male funnels long, cylindrical, with collar of same width; coelomocytes suboval or oval, slightly granular; dorsal vessel originating in XIII or XIV, blood colorless; chaetae 2−8; L = 3−6 mm; amphibious (Fig. 12.22(37)) ..... *Cernosvitoviella palustris* Healy, 1979 [western Europe]

11′ Spermathecae usually reaching X; male funnels short, cylindrical, with narrow collar; coelomocytes broadly fusiform, with acute ends, either granular or clear; dorsal vessel originating in XIII, blood either red or colorless; chaetae 4–10; L = 2.5−7 mm; amphibious (Fig. 12.22(38)) ..... *Cernosvitoviella sphaerotheca* Healy, 1975 [Ireland]

12(7) Spermathecae small; ampulla spherical, duct thick-walled, length ≥ and narrower than ampulla; vasa deferentia slightly inflated distally; coelomocytes fusiform (with or without fine points, with refractile granules), or suboval to oval, with yellow granules; dorsal vessel originating at XI/XII, blood colorless; chaetae three to seven; L = ~1.3 mm; amphibious (Fig. 12.22(41)) ..... *Cernosvitoviella microtheca* Rota & Healy, 1999 [Sweden]

12′ Spermathecae variously shaped but usually large; ampulla suboval or oval containing either ring-shaped or irregular sperm; duct subequal or up to seven times as long as ampulla; vasa deferentia not inflated distally; coelomocytes abundant, mostly broadly fusifrom, either granular or generally brown; dorsal vessel originating in XIII, blood red or colorless; chaetae 3–10; L = 2–7 mm; aquatic and in wet or moist soil. (Fig. 12.22(28, 29, 42)) ..... *Cernosvitoviella atrata* (Bretscher, 1903) [western Palaearctic. Nearctic, introduced? Variable, possibly a species complex]

Oligochaeta: Enchytraeida: Enchytraeidae: *Chamaedrilus*: Species

1 Chaetae mostly three per bundle 2

1′ Chaetae mostly two per bundle, sometimes by three posteriorly; pharyngeal glands with three pairs of dorsal lobes in V–VII, first two pairs with dorsal junctions, and two small ventral lobes in V and VI; coelomocytes small, suboval, scarcely granular; dorsal vessel beginning in 13/14; spermathecae free, ampulla pyriform; duct long, ectal pore with small gland; male funnels oval, without distinct collar, with ental aperture narrow; penial bulb small; L = 3–5 mm; amphibious ..... *Chamaedrilus hibernicus* Healy, 1975 [Ireland, Spain]

2(1) No enlarged dorsal chaetae; pharyngeal glands in 3–5 pairs, on dissepiments 4/5–8/9 3

2′ III–VII dorsal chaetae enlarged, longer and thicker; pharyngeal glands three pairs, on dissepiments 4/5–6/7, dorsal and ventral lobes present, with dorsal connections; chaetae yellowish; reproductive system in normal position, with male pores in XII; L = 5–11 mm; amphibious ..... *Chamaedrilus cognettii* (Issel, 1905) [Europe]

3(2) Pharyngeal glands with dorsal and ventral lobes 4

3′ Pharyngeal glands usually five pairs, without ventral lobes, often small; chaetae mostly three, sometimes two or, posteriorly four; asexual reproduction prevalent, most with regenerating ends; maturing seldom, reproductive system shifted forward, male pores either in VIII, IX, X, or XI; chaetae three; L = 15–25 mm; amphibious in acidic environments (Fig. 12.23(1, 2)) ..... *Chamaedrilus sphagnetorum* (Vejdovský, 1878) [Europe. Nearctic]

4(3) Pharyngeal gland pairs 3–5, at least three first pairs with dorsal and ventral lobes, large, often filling most space in respective segments; asexual reproduction prevailing, mature individuals rare, reproductive system shifted forward, with male pores either in VIII, IX, X, or XI; chaetae mostly three per bundle but anteriormost dorsal often two 5

4′ Pharyngeal glands pairs five, at 4/5–8/9, first two pairs united dorsally; small ventral lobes only in VII and VIII; clitellum not developed even in individuals with mature eggs; male pores and small penial bulbs in X; dorsal chaetae 2–3, ventral three; L = 12–15 mm ..... *Chamaedrilus valeriae* Dumnicka, 2010 [Italy]

5(4) L = 15–25 mm; amphibious (Fig. 12.23(3)) ..... *Chamaedrilus glandulosus* (Michaelsen, 1888) [Holarctic]

5′ L = 2–5 mm; in moist soil. Cryptic species genetically different from the former ..... *Chamaedrilus varisetosus* Martinsson, Rota & Erséus, 2015 [Europe]

Oligochaeta: Enchytraeida: Enchytraeidae: *Lumbricillus*: Species

In part; see also Enchytraeidae genus key, couplet 9.

1 Spermathecae consisting of fusiform ampulla and very short, indistinct ectal duct, with ectal end surrounded by glands 2

1′ Spermathecae ectal duct distinct, either bare or glandular 4

2(1) Male funnels very long, cylindrical, folded in body cavity, with wider collar; spermathecae ectal end surrounded by a crown of large glands 3

2′ Male funnels pyriform, consisting of five lobes, with narrower collar; spermathecal duct ectal pore surrounded by a crown of small glands; chaetae 3–7; L = ~8 mm; fresh and slightly brackish water; amphibious ..... *Lumbricillus fennicus* Nurminen, 1964 [Europe]

3(2) Male funnels length ~10 times width, collar 2–3 times as wide and heavily lobed; spermathecae fusiform, thick-walled, with uniform lumen, ectal end with glands; chaetae 5–12; L = 20–35 mm; marine littoral; polluted fresh water and soil (Fig. 12.23(11)) ..... *Lumbricillus rivalis* Levinsen, 1884
[Europe. Nearctic]

3′ Male funnels length ~five times width, collar wider and of regular shape; spermathecae fusiform, slightly constricted externally but with distinctly bipartite lumen; ectal half thick-walled; ental half with thinner wall, containing most of sperm; spermathecae ectal end with high, dense crown of fused glands; chaetae 2–8; L = 10–18 mm; marine littoral and polluted fresh water (Fig. 12.23(4–6)). Variable, with several polyploid forms ..... *Lumbricillus lineatus* (Müller, 1774)
[cosmopolitan]

4(1) Male funnels short, cylindrical or caliciform 5

4′ Male funnels width ≤two times length 7

5(4) Spermathecal ducts without glands; no subneural glands 6

5′ Spermathecal ampullae tubular, slightly dilated in middle portion; ducts short and with a small crown of glands; male funnels length subequal to width; three pairs of pharyngeal glands, first two with dorsal junctions; ventral lobes present, largest in third pair; subneural (copulatory) glands present in XIV; dorsal chaetae (1) 2–3 (4), ventral chaetae 3–4 (5,6); L = 3–4 mm; brackish water..... *Lumbricillus intricatus* Finogenova, 1977
[Kyrgyzstan: Lake Issyk-kul]

6(5) Spermathecal ampullae wide, ducts short and without glands; male funnels short, cylindrical, slightly longer than wide, with collar as wide; three pairs of pharyngeal glands, first pair smaller, ventral lobes present; dorsal chaetae 2–3, ventral chaetae 3–4; L = 4 mm; brackish water..... *Lumbricillus minimus* (Černosvitov, 1929)
[Kazakhstan: Lake Chalkar]

6′ Spermathecal ampullae pyriform, wide distal end abruptly separated from the short, in its middle part dilated duct; male funnels caliciform, length >1.5 times width, with slightly wider collar; three pairs of pharyngeal glands with large ventral lobes, first two pairs of dorsal lobes connected by thin threads only; dorsal chaetae 2–3 (4), ventral chaetae 2–4 (5); L = 7–12 mm (alive); branchial cavity of freshwater crabs ..... *Lumbricillus catanensis* (Drago, 1887)
[Algeria; Italy]

7(4) Spermathecae ectal duct longer than spherical or pyriform ampulla, covered with thick layer of glandular tissue different from ectal pore large crown of high glands; male funnels length >2–4 times width; pharyngeal glands three pairs, two anterior pairs dorsally connected; chaetae slightly sigmoid, 3–5 in dorsal and 4–7 in ventral bundles; L = 8–18 mm; marine littoral, terrestrial and freshwater (Fig. 12.23(7–10)). May represent a species complex ..... *Lumbricillus pagenstecheri* (Ratzel, 1869)
[Holarctic]

7′ Spermathecae ectal duct length twice width of, and narrower than, bulbiform ampulla, bare but ectal pore with small glands; male funnels length 2–3 times width; pharyngeal glands in three pairs, dorsally connected; chaetae slightly sigmoid, 2–5 in dorsal and 2–6 in ventral bundles; L = 5–6.5 mm; freshwater; known only after original description ..... *Lumbricillus kamtschatkanus* (Michaelsen, 1929)
[Russia: Lake Kurilskoe on Kamchatka Peninsula]

Oligochaeta: Enchytraeida: Enchytraeidae: *Enchytraeus* and *Marionina*: Species

1e Chaetae >two at least in some bundles 2

1′ Chaetae either paired, single, or lacking in all bundles 11

2(1) Chaetae either straight or slightly bent, arranged in symmetrical flabelliform bundles, more than three at least in some bundles 3

2′ Chaetae in bundles 2–3 5

3(2) No esophageal appendages ("peptonephridia"); very small worms, L < 5 mm 4

3′ Esophageal appendages as unbranched spongy tubes, reaching posteriorly IV; chaetae 2–5 per bundle, straight or slightly curved, obtuse; pharyngeal glands in three pairs on 4/5–6/7, with dorsal junctions, and small ventral lobes in IV–VI; spermathecal ampullae sacculate, often bipartite, ectal ducts densely glandular; L = 10–35 mm; terrestrial in decaying waste and on seashores; bred in fish hatcheries as food for fry (Fig. 12.23(22–24)). Records from freshwater can be based on other, misidentified enchytraeid species ..... *Enchytraeus albidus* Henle, 1837
[cosmopolitan]

4(3) Dorsal blood vessel from XI anteriorly; chaetae in forebody 4–7, in hindbody 2–4 (5) per bundle, straight, obtuse; spermathecal ampullae oval or suboval, ectal ducts short and narrow, glandular; L = 2–4 mm; slightly brackish water (Fig. 12.23(30–33)) ..... *Marionina brevis* Finogenova, 1972
[Ukraine: Black Sea estuaries; Caspian Sea]

4′ Dorsal blood vessel from IX anteriorly; chaetae in forebody 4−8, in hindbody 3−5 per bundle, straight and sharp, sometimes proximally slightly curved; spermathecae ampulla oval, duct short, narrow, without glands; L = 2.5−3 mm; brackish water ..... *Marionina micula* Finogenova, 1972 [Caspian Sea]

5(2) Mostly deep water in large lakes 6

5′ Either amphibious, or in shallow fresh and brackish water 7

6(5) Esophageal appendages tubular in VI; pharyngeal glands three pairs; dorsal blood vessel beginning in VIII; spermathecal ampullae prolonged, ectal ducts subequal in length to ampullae, thick-walled, ectal pore with gland; chaetae *baciliform,* obtuse, slightly curved proximally, anterior ventral bundles three, elsewhere two per bundle; body subcompressed laterally; L = 7−8 mm; freshwater ..... *Enchytraeus platys* Semernoy, 1980 [Mongolia: Lake Hubsugul]

6′ Esophageal appendages in IV tubular with folded walls; pharyngeal glands 2−3 pairs in IV–V or IV–VI, with ventral lobes; dorsal blood vessel beginning either in 8/9 or XII; spermathecae with oval ampulla and separate, glandular ectal duct; chaetae two (3) per bundle, straight, distally thinner; L = 6−7 mm; brackish water ..... *Enchytraeus issykkulensis* Hrabě, 1935 [Kyrgyzstan: Lake Issyk-kul]

7(5) Chaetal bundles present in all anteclitellar segments 8

7′ Dorsal chaetae lacking in II (or also III) 10

8(7) Pharyngeal glands three pairs, without dorsal junctions 9

8′ Pharyngeal glands three pairs, in IV–VI (the last pair reaching VII), with dorsal junctions; spermathecae length ~four times width, small suboval ampulla and thick-walled ectal duct subequal in width; external pore ringed with glands; chaetae two, III seldom ventrally three; L = 3−4 mm; slightly brackish water ..... *Marionina mica* Finogenova, 1972 [Ukraine: Black Sea estuaries; Caspian Sea]

9(8) Spermathecae ampullae fusiform or pyriform; both ducts very short and obscure; ectal duct with small glandular cells; spermathecal pore glands of varying sizes; esophagus chloragogen tissue from V (separate cells present already in IV); L = 5−10 mm; terrestrial, sometimes also in freshwater (Fig. 12.23(25−28)) ..... *Enchytraeus buchholzi* Vejdovský, 1879 [Holarctic. Neotropics]

9′ Spermathecae with well-differentiated ampulla; ectal duct longer than ampulla, densely glandular; spermathecal pore may have small glands; esophagus chloragogen tissue dense from VII (but weakly developed already in V); L = ~3 mm; terrestrial, sometimes also in freshwater (Fig. 12.23(29)) ..... *Enchytraeus christenseni* Dózsa-Farkas, 1992 [Holarctic]

10(7) Spermathecal ampullae surrounded by 7−8 short diverticula; coelomocytes discoid to oval; dorsal bundles lacking in II or II–III; chaetae two (3) per bundle; L = 8−10 mm; marine and brackish-water littoral, seldom freshwater (Fig. 12.23(34−36)) ..... *Marionina southerni* (Černosvitov, 1937) [Holarctic]

10′ Spermathecal ampullae without diverticula, ovoid or suboval, either connected with esophagus or not; coelomocytes ovoid; chaetae two (3) per bundle, dorsal bundles lacking in II; L = 4−7 mm; terrestrial, amphibious and in freshwater (Fig. 12.23(37)) ..... *Marionina argentea* (Michaelsen, 1889) [Holarctic]

11(1) Chaetae in most bundles paired (two per bundle), straight with proximal hook (also many terrestrial species with this character, not included into the key) 12

11′ Chaetae only single per bundle or lacking 17

12(11) Dorsal chaetae present in all preclitellar bundles from II 13

12′ Dorsal chaetae lacking in II(III), or in other segments 14

13(12) Spermathecae with prolonged suboval ampulla, its sharp ental end connected with esophagus; distinct ectal duct thick-walled; large gland at spermathecal pore; L = 3 mm; brackish water ..... *Marionina aberrans* Finogenova, 1973 [Caspian Sea]

13′ Spermathecal ampullae round or oval, with irregular lumen and sperm arranged in distinct rings mostly at wall; short ectal duct bearing glands of varying size, the largest near the ectal pore; L = 2−6.5 mm; marine littoral ..... *Marionina coatesae* Erséus, 1990 [Japan]

14(12) Dorsal chaetae lacking in IX−XI, or in all segments 15

14′ Chaetae lacking dorsally in II but paired in all or most other segments 16

15(12) Dorsal bundles lacking in IX–XI and only one chaeta in VII–VIII; two chaetae remaining bundles; all pharyngeal glands with dorsal connections; IV esophageal appendages clavate, hollow; spermathecae with small pyriform ampulla and long, glandular ectal duct, but no glands at distal end; ampullae ental ends join dorsally before communication with esophagus; L = ~6 mm; terrestrial and amphibious. ..... *Marionina clavata* Nielsen & Christensen, 1961 [Europe. Nearctic]

15′ No dorsal chaetae; ventral chaetae (1) two in anteclitellar and one in posterior segments but lacking in XI–XIII; pharyngeal glands three pairs, anterior pairs at 4/5 and 5/6 merging dorsally and with small ventral lobes; spermathecal ampullae oval, internally divided into several lobes by longitudinal septa(?); ectal ducts short, surrounded by small irregular gland cells becoming higher near ectal pore; L = 5−7 mm; freshwater ..... *Marionina biwaensis* Torii, 2012
[Japan: Lake Biwa]

16(14) Three pairs of pharyngeal glands on 4/5 to 6/7, anterior two pairs united dorsally, posterior two pairs with ventral lobes; spermathecae with simple fusiform, thick-walled ampulla, with distinct ental and ectal ducts, the latter surrounded by glands of irregular size, not forming any basal crown; L = 4−6 mm; marine littoral and freshwater..... *Marionina charlottensis* Coates, 1980
[Russia: Lake Kurilskoe on Kamchatka Peninsula. Nearctic]

16′ Pharyngeal glands as unpaired dorsal lobes in IV and V, a pair of ventral lobes in VI; spermathecae with spherical or oval ampulla attached to esophagus, and ectal duct with straight canal and undulating outer surface, without glands; L =1.5 mm; caves and groundwater ..... *Marionina sambugarae* Schmelz, 2015
[France]

17(11) Chaetae one per bundle, present at least in some anterior segments..... 18

17′ Chaetae completely lacking 19

18(17) Chaetae present in all or most segments, one per bundle (but lacking in some individuals), straight and obtuse; two pairs of pharyngeal glands with dorsal and ventral lobes, in IV–V; esophageal appendages in IV, tubular with folded walls; dorsal blood vessel beginning in VIII; male funnel length ≤2.5 times width; spermathecae with oval ampulla and separate, glandular ectal duct covered; only 20 segments, thus postclitellar region very short; L = 5 mm; brackish water..... *Enchytraeus przewalskii* Hrabě, 1935
[Kyrgyzstan: Lake Issyk-kul]

18′ Chaetae singular in ventral bundles of II–V, lacking elsewhere, straight and obtuse with proximal hook; pharyngeal glands four pairs, at 4/5 and 5/6, and in VI and VII, those of two first pairs joining dorsally, all with ventral lobes; male funnels length 2−4 times width; with narrower collar; spermathecal ampullae with irregular diverticula at ectal edge (not seen in the lacustrine individuals); ectal duct short, surrounded by small, irregular gland cells; those near ectal pore are longer than the rest and can form a crown; L = 4−9 mm; marine littoral, freshwater (Fig. 12.23(38−40))..... *Marionina klaskisharum* Coates, 1983
[Russia: Lake Kurilskoe on Kamchatka Peninsula. Nearctic]

19(17) Pharyngeal glands three pairs, those in IV/V and V/VI united dorsally, third pair free, all with ventral lobes, the largest ventral lobes in VI; male funnels cylindrical, length 4−6 times width, with collar of subequal width; spermathecal ampullae irregularly round or oval, ducts small and surrounded by irregular gland cells longest at ectal pore; L = 4.5−7 mm; marine littoral; freshwater ..... *Marionina nevisensis* Righi & Kanner, 1979
[Japan: Lake Biwa and Takatoki River. Circumtropical]

19′ Tiny terrestrial worms very seldom occurring in fresh water; not included in the key..... *Achaeta*

Oligochaeta: Enchytraeida: Enchytraeidae: *Henlea*: Species

1 Intestine beginning in IX, intestinal diverticula present in VIII beside esophagus; chaetae in fan-like bundles subequally long and thick, distal ends aligning in one line..... 2

1′ Intestine beginning in VIII, without diverticula; chaetae aciculate, distally tapering, 3−6 in dorsal bundles, 4−8 in ventral bundles; the medium chaetae in each bundle shorter but distal ends aligning with the rest; no intestinal appendages; dorsal blood vessel beginning in VIII; spermathecal ampullae tubular, without diverticula, ental ends join to form short common duct communicating with esophagus dorsally; spermathecal pores may have sparse glands; oval coelomocytes often abundant; L = 5−10 mm; amphibious (Fig. 12.23(18, 19))..... *Henlea perpusilla* Friend, 1911

2(1) Several separate intestinal appendages present..... 3

2′ VIII with one integrated, cuff-like intestinal appendage surrounding esophagus; chaetae 5−8 in anterior dorsal and 6–10 in ventral bundles, the number decreasing to two in hindbody; pharyngeal glands with three pairs of free dorsal lobes in V–VII and two pairs of ventral lobes in VI and VII; dorsal vessel beginning in IX; spermathecal ampullae tubular, joining before dorsally falling into esophagus; ectal ducts short, pores surrounded with several glands; male funnels oval, with narrow collar; penial bulbs small; L = 9−13 mm; freshwater streams ..... *Henlea andreae* Rodriguez & Giani, 1986
[Spain]

3(2) VIII with two intestinal diverticula, not coalescent with esophagus; IV with large lobate esophageal appendages; dorsal blood vessel beginning in VIII; 1−2 large eggs at a time; chaetae 3−8 in dorsal and 4−8 in ventral bundles; L = 12−30 mm; amphibious. ..... *Henlea nasuta* (Eisen, 1878)
[Holarctic]

3′ Four intestinal diverticula closely applied to one another and to esophagus, resembling a kind of ventriculus divided by longitudinal septa; dorsal blood vessel beginning in the anterior portion of IX; one up to eight large eggs; chaetae 4−8 in dorsal and 5−10 in ventral bundles; L = 10−15 mm; freshwater and amphibious (Fig. 12.23(15−17)) ..... *Henlea ventriculosa* (Udekem, 1854) [nearly cosmopolitan]

Oligochaeta: Crassiclitellata: Families

Consists mostly of terrestrial, including some accidentally falling into water; also present are some freshwater and amphibious species.

1 Clitellum beginning before XX, covering the male pores at least with its anterior edge 2

1′ Paired male pores in XV (seldom in XII, XIII, or XIV), conspicuous, often on glandular swellings; clitellum beginning not before XX, always bearing a pair of ventrolateral pubertal ridges or series of pubertal tubercles; female pores in XIV inconspicuous, alike the numerous spermathecal pores when present; mainly terrestrial ..... **Lumbricidae [p. 454]**

2(1) Male pores on glandular swellings in XIII or XV, bourne anteriorly on the long annular clitellum with inconspicuous borders; female pores inconspicuous; spermathecae absent, external spermatophores exchanged at copulation; freshwater 3

2′ Male pores more posterior; freshwater and terrestrial 4

3(2) Male pores in XV (Fig. 12.28(12−14)) ..... **Criodrilidae**, one species: *Criodrilus lacuum* Hoffmeister, 1845 [Europe, Mediterranean Basin, central Asia]

3′ Male pores in XIII ..... **Biwadrilidae**, one species; *Biwadrilus bathybates* (Stephenson, 1917) [Japan]

4(2) Male pores in XVII or XVIII, inconspicuous or on small protuberances, very prominent prostate pores can lie in the same or neighboring segments; female pore(s) in XIV either paired or single, often conspicuous; clitellum annular, covering genital pores; spermathecal pores in 7/8 and/or 8/9, or lacking; mostly terrestrial 5

4′ Male pores in XIX on long transparent pubertal ridges bordering the saddle-shaped clitellum, inconspicuous; female pores in XIV inconspicuous, as are spermathecal pores on 6/7−8/9; no modified genital chaetae; freshwater (Fig. 12.28(15, 16)) ..... **Sparganophilidae**, one species: *Sparganophilus tamesis* Benham, 1892 [western Europe. Nearctic]

5(4) No modified genital chaetae; esophageal diverticula present or lacking 6

5′ Modified penial chaetae present at male pores; no modified esophageal diverticula in IX ..... **Benhamiidae**, one genus: ***Dichogaster*** **[p. 457]**

6(5) Clitellum reduced to 3.5−5 segments, from XIII to XVIII at most; posterior location of male pores relative to the clitellum, in XVIII; no esophageal diverticula; up to 50 chaetae per segment, in a perichaetine arrangement; L = 80−93 mm; fast running waters ..... **Megascolecidae,** one species: *Perionyx fluviatilis* Nesemann, 2007 [Nepal]

6′ Clitellum extending more than five segments, from XIII or XIV to XVIII−XIX; male pores in clitellate segments; paired simple-pointed chaetae as in the lumbricids; one pair of modified esophageal diverticula in IX ..... **Ocnerodrilidae [p. 457]**

Oligochaeta: Crassiclitellata: Lumbricidae: Genera

1 *Prostomium epilobous*, the prostomium appendage not reaching intersegmental furrow 1/2; seldom this appendage lacking; male pores mostly in XV (*Eiseniella* often in XIII or other segments) 2

1′ *Prostomium tanylobous*, its flat appendage reaching on peristomium dorsal side to 1/2; clitellum in XXVI, XXVII–XXXI, XXXII, tubercula pubertatis ridge-shaped in XXVIII–XXXI, male pores in XV; dark violet pigment particulary in forebody, tail often flattened; L = 33−150 mm; terrestrial, occasionally falling into water (Fig. 12.28(1−3)) ..... *Lumbricus rubellus* Hoffmeister, 1843 [Palaearctic]

2(1) Saddle-shaped clitellum ventrolateral edges with tubercula pubertatis mostly represented by 2−3 suboval protuberances with margins meeting 3

2′ Tubercula pubertatis represented by continuous ridges 4

3(2) Tubercula pubertatis in XXXI, XXXIII. and XXXV as rows of three sucker-shaped protuberances; clitellum in XXIX, XXX–XXXVII; mostly yellowish green but sometimes pink; L = 26−85 mm. Terrestrial and amphibiotic (Fig. 12.28(4)) ..... *Allolobophora chlorotica* (Savigny, 1826) [Palaearctic]

3′ Tubercula pubertatis consisting of two half-integrated protuberances ..... ***Aporrectodea*** [in part; **p. 455**]

4(2) Clitellum more anterior, its posterior edge not reaching XLVII 5

4′ Clitellum in XXXVI, XXXVII–XLVII, XLVIII; amphibious, in temporarily inundated places; lower Danube region ..... ***Aporrectodea*** [in part; **p. 455**]

5(4) Clitellum shorter than nine segments 6

5′ Clitellum very long, 9–13 segments, tubercula pubertatis relatively short ..... ***Helodrilus*** **[p. 455]**

6(5) Clitellum posterior edge reaching backwards not more than to XXX; male pores in XIII or XV 7

6′ Clitellum posterior edge reaching farther backwards than XXX; male pores always in XV 8

7(6) Chaetae widely separated; pigmentation purple brown, IX–XII unpigmented; male pores in XV without glandular pads; ventral chaetae in IX–XI (XII) and XXV–XXX on glandular tumescenses; IX modified genital chaetae, longer and straighter than the rest, distally trihedral; clitellum in XXIII to XXV–XXX, tubercula pubertatis in XXVI– XXVIII, XXIX; L = 40–108 mm; terrestrial and amphibious ..... ***Dendrobaena*** [in part; **p. 456**]

7′ Chaetae closely paired, hindbody quadrangular ..... ***Eiseniella*** **[p. 456]**

8(6) Chaetae broadly spaced or equidistant from each other 9

8′ Chaetae closely paired 10

9(8) Chaetae broadly spaced; clitellum in XXV XXVII– XXX. . . XXIII; tubercula pubertatis XXVIII, XXIX–XXX, XXXI, sometimes weakly developed and obscure; male pores small; color red-violet, forebody and dorsal side darker; L= 14–60 mm; terrestrial, accidentally in fresh water ..... *Dendrodrilus rubidus* (Savigny, 1826) [Palaearctic]

9′ All eight segment chaetae equidistant from each other, hindbody octagonal; clitellum in XXVII. . . XXX– XXXIII, XXXIV; tubercula pubertatis in XXXI–XXXIII; male pores of variable size; color red-violet, forebody darker; L= 16–60 mm; terrestrial, accidentally in fresh water ..... ***Dendrobaena*** [in part; **p. 456**]

10(8) Clitellum longer and located between XXIII and XXXIV 11

10′ Clitellum occupying six segments, XXX–XXXV; tubercula pubertatis in XXX, XXXI–XXXIV, XXXV; usually whitish but sometimes with dark pigmentation; L = 24–180 mm; terrestrial, often in wet soil ..... *Octolasion lacteum* Örley, 1881 [Palaearctic]

11(10) Unpigmented, pink worms; terrestrial, accidentally in fresh water ..... ***Aporrectodea*** [in part; **p. 455**]

11′ Usually pigmented, worms, sometimes striped or with lighter spots ..... ***Eisenia*** **[p. 456]**

Oligochaeta: Crassiclitellata: Lumbricidae: *Aporrectodea*: Species

1 Saddle-shaped clitellum ventrolateral edges with tubercula pubertatis mostly represented by 2–3 suboval protuberances with margins meeting 2

1′ Tubercula pubertatis represented by continuous ridges 3

2(1) Tubercula pubertatis in XXXI and XXXIII, clitellum in XXVII, XXIX–XXXIV, XXXV; color gray or pink, clitellum brownish; terrestrial, very common, occasionally falling into water (Fig. 12.28(5, 6)) ..... *Aporrectodea caliginosa* (Savigny, 1826) [Palaearctic]

2′ Tubercula pubertatis in XXXIII and XXXIV, clitellum in XXVIII, XXIX –XXXV, XXXVI; color gray; L = 40–100 mm; amphibious ..... *Aporrectodea limicola* (Michaelsen, 1890) [western Europe]

3(1) Unpigmented, pink worms; clitellum in XXIII XXVI–XXXI XXXIV; tubercula pubertatis in XXVIII, XXIX –XXX, XXXI; clitellum and male pores glandular papillae often very thick; L = 20–150 mm; terrestrial, accidentally in fresh water ..... *Aporrectodea rosea* (Savigny, 1826) [Palaearctic]

3′ Clitellum in XXXVI, XXXVII–XLVII, XLVIII; tubercula pubertatis as slight bands in XLIII, XLIV–XLVII, XLVIII; reproductive characters appearing for a very short period; color dark green; L = 120–250 mm; amphibious, in astatic wetlands ..... *Aporrectodea dubiosa* (Örley, 1880) [lower Danube region]

Oligochaeta: Crassiclitellata: Lumbricidae: *Helodrilus*: Species

1 Clitellum covering 11–13 segments 2

1′ Clitellum occupying nine segments, XXII, XXIII–XXX, XXXI, tubercula pubertatis short but large in XXIX only, spermathecae lacking; no glandular pads at male pores; hindbody flattened quadrangularly; mostly unpigmented but forebody light brown; L = 60–70 mm; freshwater or amphibious ..... *Helodrilus hachiojii* Blakemore, 2007 [Japan]

2(1) Tubercula pubertatis occcupying more than two segments; body unpigmented, without dark markings 3

2′ Clitellum in XXI, XXII–XXXII, XXXIII, tubercula pubertatis very short, in XXIX, XXX–XXX, XXXI, sometimes extending into neighboring segments; male pores in XV with large glandular papilla; body unpigmented but with scattered dark markings; L = 35−80 mm (Fig. 12.28(7)); freshwater and amphibious ..... *Helodrilus oculatus* Hoffmeister, 1845 [Europe; Transcaucasia]

3(2) Clitellum in XXI. . . XXIII–XXXIII, XXXIV, tubercula pubertatis in ½XXIX, ½XXX–XXXII, ½XXXIII; male pores with glandular pad; L = 28−135 mm; freshwater and amphibious..... *Helodrilus patriarchalis* (Rosa, 1893) [Europe; Transcaucasia; Near East]

3′ Clitellum in XXV–XXXV, tubercula pubertatis in XXXI–½XXXIV; male pores without glandular pad; L = 65−95 mm; freshwater ..... *Helodrilus mozsaryorum* (Zicsi, 1974) [Hungary]

Oligochaeta: Crassiclitellata: Lumbricidae: *Dendrobaena*: Species

1 Chaetae widely separated; pigmentation purple brown, IX–XII unpigmented; male pores in XV without glandular pads; ventral chaetae in IX–XI (XII) and XXV–XXX on glandular tumescenses; IX modified genital chaetae, longer and straighter than the rest, distally trihedral; clitellum in XXIII. . . XXV–XXX, tubercula pubertatis in XXVI− XXVIII, XXIX; L = 40−108 mm; terrestrial and amphibious ..... *Dendrobaena byblica* (Rosa, 1898) [Europe; Near East; central Asia]

1′ Chaetae subequidistant from each other, hindbody octagonal; clitellum in XXVII XXX– XXXIII, XXXIV, tubercula pubertatis in XXXI–XXXIII; male pores of variable size; color red-violet, forebody darker; L = 16−60 mm; terrestrial, accidentally in fresh water..... *Dendrobaena octaedra* (Savigny, 1826) [Palaearctic]

Oligochaeta: Crassiclitellata: Lumbricidae: *Eiseniella*: Species

1 Clitellum annular, beginning from XX–XXIII 2

1′ Clitellum always saddle-shaped, beginning farther backward than XXIII 4

2(1) Prostomium epilobous; modified genital chaetae unknown 3

2′ Prostomium prolobous or zygolobous (without the dorsal appendage on I); male pores either in XIII or XV, glandular pads weak; clitellum in (½XX)XXI –XXVI (XXVII, ½XXVIII), tubercula pubertatis in XX–XXV, XXVI; ventral chaetae of IX, XXI, and XXVII on glandular tumescenses, those of IX modified as genital chaetae; L = 40−62 mm; freshwater ..... *Eiseniella ochridana* Černosvitov, 1931 [Albania/Macedonia: Lake Ohrid]

3(2) Clitellum in XX, XXI–XXIV, XXV, tubercula pubertatis in XXI–½XXIV (XXIV), male pores in XIII; L ≤ 80 mm; amphibiotic .... *Eiseniella neapolitana* (Örley, 1885) [southern Europe; Near East]

3′ Clitellum in XXII–XXVI or XXIII–XXVII, tubercula pubertatis in XXIII–XXV or XXIV– XXVI, respectively; male pores large, usually in XIII but sometimes in XI, XII, XIV, or XV, often asymmetrical; brown pigment present; L = 20−80 mm; freshwater and amphibious (Fig. 12.28(8−11))..... *Eiseniella tetraedra* (Savigny, 1826) [cosmopolitan]

4(1) No enlarged chaetae; clitellum posterior edge reaching XXX or XXXI 5

4′ Chaetae large and hooked in VI–VIII and in caudal segments, closely paired; clitellum in XXIV–XXIX, tubercula pubertatis as thin ridges in XXVI–½XXVIII; L = 58−113 mm; amphibious ..... *Eiseniella oltenica* (Pop, 1938) [southern Europe]

5(4) Clitellum in XXIV, XXV–XXX, tubercula pubertatis in XXVI–XXIX, male pores in XV moderately sized; L = 40−100 mm; freshwater and amphibious..... *Eiseniella balcanica* Černosvitov, 1931 [central Europe]

5′ Clitellum in XXV–XXXI, tubercula pubertatis in XXVII–XXIX; male pores on very large glandular pads; glandular tumescenses surrounding ventral chaetae in X, XVI, and XXVI–XXX, as well as dorsal chaetae in X and XI; prostomium pro-epilobic, tail region quadrangular; L = 42−50 mm; freshwater or amphibious..... *Eiseniella koreana* Zicsi, 1972 [Korea]

Oligochaeta: Crassiclitellata: Lumbricidae: *Eisenia*: Species

1 Usually dark brown pigmentation present, with large unpigmented spots in IX–XI 2

1′ Color yellowish-violet, paler ventrally, or forebody with darker transverse stripes; clitellum in XXIV. . . XXVII–XXXII. . . XXXIV, tubercula pubertatis in XXVII. . . XXIX–XXXI, XXXII; male pores with moderate glandular pads; L = 55−110 mm; freshwater and amphibious..... *Eisenia spelaea* (Rosa, 1901) [southern Europe]

2(1) Male pore glandular pads in XV but reaching XVI; clitellum in XXVI, XXVII–XXXIII, tubercula pubertatis in XXX–1/3 XXXIII; dorsal and ventral chaetae in XI on glandular tumescenses; L = 45−150 mm; amphibious ..... *Eisenia hydrophilica* Kvavadze, 1979 [Transcaucasia]

2′ Male pores in XV on small pads; clitellum in XXVI, XXVII –XXXIII, XXXIV; tubercula pubertatis in ½XXVIII, XXIX –XXXI; clitellar region and neighboring segments ventral chaetae on glandular tumescenses; pigmentation variable, pale forms exist; L = 25−150 mm; terrestrial, accidentally in fresh water..... *Eisenia nordenskioldi* (Eisen, 1879) [eastern and central Palaearctic]

Oligochaeta: Crassiclitellata: Benhamiidae: *Dichogaster*: Species

1 Two pairs of prominent prostata pores connected by two longitudinal seminal grooves in XVII and XIX, along ventral chaetae line; a pair of acute genital chaetae at each pore; paired male pores in the seminal grooves in XVIII; single female pore on a papilla midventral in XIV; L = 19−40 mm; terrestrial, in Europe in sewer pipes (Fig. 12.28(17−19)) ..... *Dichogaster bolaui* (Michaelsen, 1891) [introduced: Finland, Ireland and Sweden. Circumtropical]

2′ One pair of prostata pores in XVII, accompanied by pairs of distally knobbed genital chaetae; male pores in XVII on closely paired porophores; female pores in XIV small and closely paired ventrally; L = 17−70 mm; terrestrial, in Europe in sewer pipes .... *Dichogaster saliens* (Beddard, 1893) [introduced: Sweden. Circumtropical]

Oligochaeta: Crassiclitellata: Ocnerodrilidae: Genera and Species

1 Male pores on small protuberances in XVII; prostates open into male pores; inconspicuous female pores in XIV; no spermathecal pores; forebody dark and iridiscent, otherwise colorless; L = 12−37 mm (Fig. 12.28(20)); amphibious .... *Ocnerodrilus occidentalis* Eisen, 1878 [cosmopolitan]

1′ Ventral surface concave in XVII−XIX; concavity margins bear small male pores in XVIII, prostate glands pores in XVII and XIX on smaller tubercles surrounded by a circular ridge; inconspicuous female pores ventrally in XIV, spermathecal pores dorsally in VII/VIII and VIII/IX; unpigmented, anterior end may be iridescent; L = 20−95 mm; amphibious (Fig. 12.28(21)) .... *Eukerria saltensis* (Beddard, 1895) [introduced: Europe, Japan. Cosmopolitan]

Oligochaeta: Lumbriculida: Families

1 Male ducts plesiopore; male pores in X, spermathecal pores in X and/or XI; chaetae always simple-pointed .... **Dorydrilidae**, one genus; ***Dorydrilus*** **[p. 457]**

1′ Male ducts prosopore or semiprosopore; males pores 1−2 pairs, usually in X or IX−X, sometimes in VIII, seldom in multiple pairs; spermathecal pores immediately before or/and after them in neighboring segments; chaetae simple-pointed or with shorter upper tooth, seldom lacking..... **Lumbriculidae [pp. 457, 471]**

Oligochaeta: Lumbriculida: Dorydrilidae: *Dorydrilus*: Species

1 One single pair of spermathecae..... 2

1′ Spermathecae two pairs, with pores in X and XI; atria pyriform, distal portion may be protruded as pseudopenis; L = ~15 mm .... *Dorydrilus tetrathecus* Hrabě, 1960 [Germany]

2(1) Spermathecal pores in X, the same segment with male pores; pseudopenes large, often protruded in preserved specimens; L = 8−15 mm (Fig. 12.26(30))..... *Dorydrilus michaelseni* Piguet, 1913 [Europe]

2′ Spermathecal pores in XI; pseudopenes always internal; L = 13−17 mm ..... *Dorydrilus mirabilis* Hrabě, 1936 [Switzerland]

Oligochaeta: Lumbriculida: Lumbriculidae: Genera (excluding Lake Baikal)

A separate key to Lumbriculidae of Lake Baikal is given on p. 471.

1 Proboscis (tentacle) on prostomium present (but see exception in 3); spermathecae connected with esophagus in most species 2

1′ No tentacle; no connection between spermathecae and esophagus 4

2(1) All chaetae simple-pointed..... 3

2′ All or many chaetae with small or rudimentary upper tooth. Spermathecae connected with esophagus ..... ***Rhynchelmis*** [in part; **p. 460**]

3(2) Both male and spermathecal pores in IX, close together; no connection between spermathecae and esophagus; L = 50–65 mm; caves (Fig. 12.24(20)) ..... *Guestphalinus wiardi* (Michaelsen, 1933) [Germany]

3′ Male pores in X, spermathecal pores in IX or in VIII and IX; spermathecae connected with esophagus ..... ***Rhynchelmis*** [in part; **p. 460**]

4(1) All or most chaetae with shorter upper tooth 5

4′ All chaetae simple-pointed (seldom lacking) 8

5(4) Spermathecae present 6

5′ Spermathecae lacking; atria in X, pyriform, very muscular ..... ***Trichodrilus*** [in part; **p. 463**]

6(5) Spermathecae in postatrial segment(s) 7

6′ Spermathecae before atrial segment. Usually two pairs of testes in IX and X, atria in X ..... ***Stylodrilus*** [in part; **p. 461**]

7(6) Body usually several cm long, pigmented; living mostly in standing water, able to swim short distance; male pores mostly on prominent porophores; architomy present at least in some species, connected with variations in the number and location of reproductive organs ..... ***Lumbriculus*** [in part; **p. 462**]

7′ Body usually up to 15 mm long, unpigmented, living mostly in clean streams; male pores in IX, on porophores or without them ..... ***Trichodrilus*** [in part; **p. 463**]

8(4) Both male and female reproductive organs present 9

8′ Male reproductive organs lacking, spermathecae present but not functioning ..... ***Eumuliercula*** **[p. 467]**

9(8) Atrium and spermatheca unpaired, with ventromedial male pore in X and spermathecal pore in VIII or IX 10

9′ Atria and spermathecae paired 11

10(9) Atrium thin-walled. Spermatheca in VIII or lacking ..... ***Tatriella*** **[p. 467]**

10′ Atrium with very thick muscular wall covered with prostatic cells; spermathecal pore in IX (sometimes another also in VIII); blind lateral blood vessels, one pair per segment, covered with dark chloragogen cells, in midbody; two pairs of blind lateral vessels per segment more caudad, with numerous small appendages; swimming; L = 35–50 mm ..... *Eclipidrilus lacustris* (Verrill, 1871) [western Europe. Nearctic]

11(9) Vasa deferentia open into male pores via atria 12

11′ Testes and male funnels in VIII and IX; additional, rudimentary male funnels in VII; atria in VIII rudimentary, not connected with vasa deferentia or male pores; male pores in IX immediately receiving both vasa deferentia of one side; small copulatory glands in VII–X; spermathecae one pair in VII, with long sacculate ampulla, short duct and lateral pore; L = 27–32 mm ..... *Kurenkovia magna* Sokolskaja, 1969 [Russia: Kamchatka]

12(11) Male ducts semiprosoporous (two testes and vasa deferentia per atrium) 13

12′ Male ducts prosoporous (one atrium and vas deferens per atrium) 18

13(12) Spermathecae postatrial; atria in X (seldom in IX) 14

13′ Spermathecae preatrial; atria in IX or X 17

14(13) The first or single pair of spermathecae in atrial segment X 15

14′ Spermathecae 1–2 pairs, always only in postatrial segments (X or XI and/or XII) 16

15(14) Long, tubular atria filling X–XII, with one male pore in X and another in XI; spermathecae in X, with ventral pores near X/XI; L = ? (probably abnormal specimen); in caves ..... ***Trichodrilus*** [in part; **p. 463**]

15′ Spermathecae 2–3 pairs, the first pair in the atrial segment X ..... ***Cookidrilus*** **[p. 467]**

16(14) Spermathecae in XII, with very long ampulla and ventrolateral pore; L ≤ 25 mm (Fig. 12.25(3, 4)) ..... ***Lumbriculus*** [in part; **p. 462**]

16′ Spermathecae in X or XI, or in XI and XII, pores ventral; smaller worms ..... ***Trichodrilus*** [in part; **p. 463**]

17(13) Atria opening with male pores in X, spermathecae in VIII ..... ***Pseudorhynchelmis*** **[p. 467]**

17′ Atria and male pores in X (seldom in XI), spermathecae in IX (or X, respectively, or lacking) ..... ***Stylodrilus*** [in part; **p. 461**]

18(12) Atria and male pores one pair, in X 19

18′ Atria and male pores two pairs, in X and XI, or one pair in VII, VIII, or IX 22

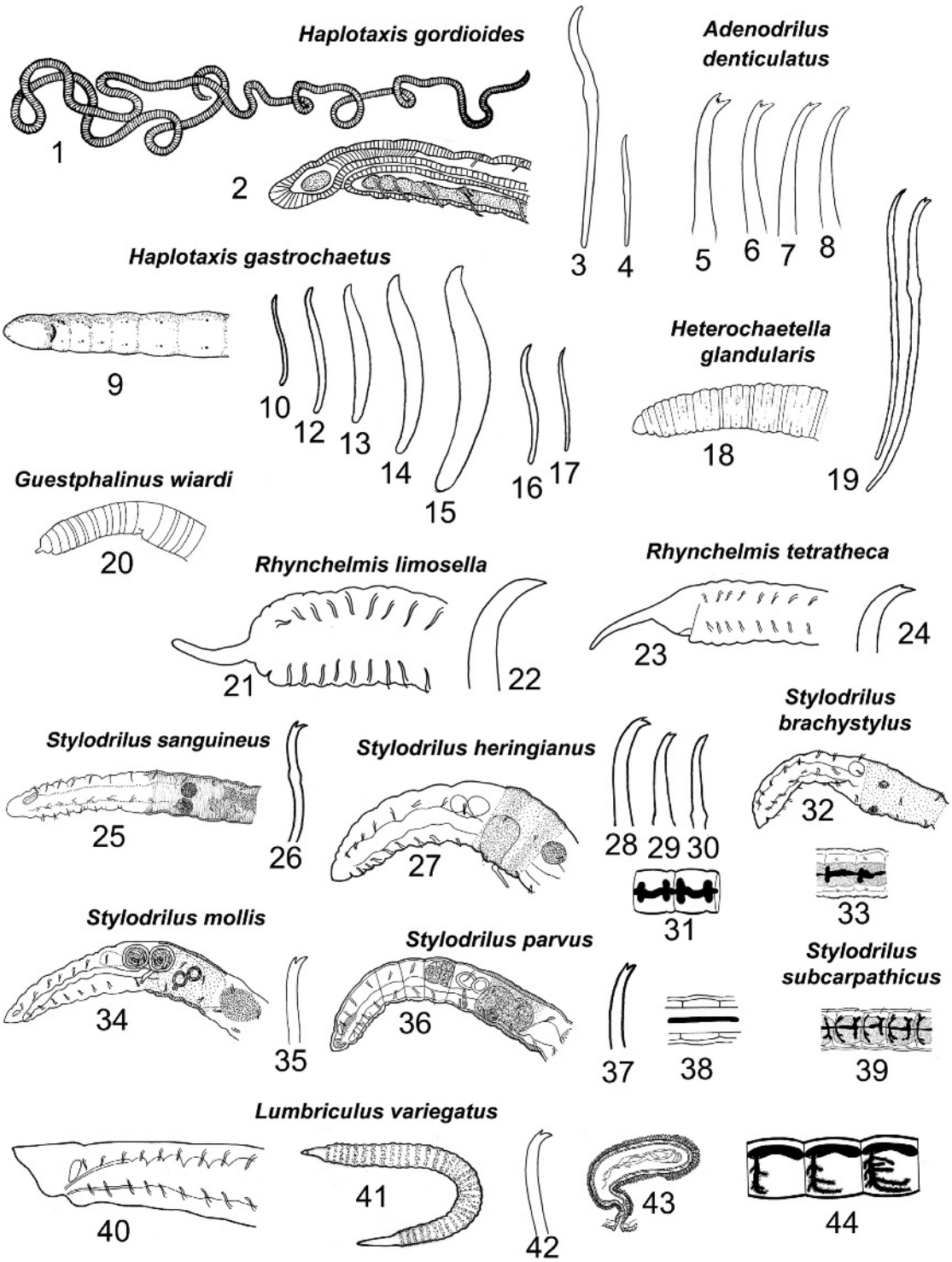


FIGURE 12.24 Haplotaxidae and Lumbriculidae I: (1–4): *Haplotaxis gordioides*: (1) general view, (2) anterior end, (3) ventral chaeta, (4) dorsal chaeta; (5–8): *Adenodrilus denticulatus*, chaetae; (9–17): *Haplotaxis gastrochaetus:* (9) anterior end, (10–13): sequential chaetae from forebody, (14, 15) chaetae from midbody, (16, 17) posterior chaetae; (18, 19) *Heterochaetella glandularis*: (18) anterior end, (19) chaetae; (20) *Guestphalinus wiardi*, forebody of sexually mature specimen with clitellum; (21, 22) *Rhynchelmis limosella*: (21) anterior end, (22) chaeta; (23, 24) *Rhynchelmis tetratheca*: (23) anterior end, (24) chaeta; (25, 26) *Stylodrilus sanguineus:* (25) forebody of sexually mature specimen with clitellum, (26) chaeta; (27–31): *Stylodrilus heringianus*: (27) forebody of sexually mature specimen with clitellum, (28–30): chaetae, (31) posterior blood vessels; (32, 33) *Stylodrilus brachystylus*: (32) forebody of sexually mature specimen with clitellum, (33) posterior blood vessels; (34, 35) *Stylodrilus mollis:* (34) forebody of sexually mature specimen with clitellum, (35) chaeta; (36–38): *Stylodrilus parvus*: (36) forebody of sexually mature specimen with clitellum, (37) chaeta, (38) posterior dorsal blood vessel; (39) *Stylodrilus subcarpathicus*, posterior blood vessels; (40–44): *Lumbriculus variegatus*: (40) anterior end, (41) fragment with regenerating ends, (42) chaeta, (43) atrium, (44) posterior blood vessels in lateral view.

19(18) Spermathecae postatrial; male pores on small papillae, without penes 20

19′ Male pores in X, spermathecal pores in IX, ventral; vasa deferentia short and thick, falling into apical end of atrium; atrial ampulla small, thick-walled, suboval, ectal duct broad with thick epithelium similar to a penial sac; spermathecal ampullae large suboval, ducts short, with a medial extension; swimming; L = 70−80 mm; groundwater ..... *Hrabea ogumai* Yamaguchi, 1936 [Japan]

20(19) Male pores and atria in X, spermathecal pores in XII; atria long tubular 21

20′ Male pores and atria in X, spermathecal pores in XI; atria clavate with short ectal duct; no copulatory glands; spermathecae with irregular ampulla reaching XII, and narrow duct; segment XI ventrally flattened; L = 7−11 mm ..... *Yamaguchia toyensis* Fend & Ohtaka, 2004 [Japan]

21(20) Large copulatory glands posterior to male pores; spermathecae in XII, small; L ≥ 35 mm ..... *Teleuscolex grubei* Michaelsen, 1901 [Russia: Lake Baikal and Angara River in Siberia]

21′ Atria and male pores two pairs, in X and XI, or one pair in VII, VIII, or IX; no copulatory glands; spermathecae with large ampulla reaching up to XIV–XV; anterior chaetae thinner and more curved; L = 21−27 mm ..... ***Lamprodrilus*** [in part; **p. 469**]

22(18) Atria and male pores two pairs, in X and XI (with rare exceptions), spermathecae in XIII (in one case in XIV) 23

22′ Atria and male pores one or two pairs in VII, VIII, or IX, spermathecae may lie either before or after atrial segment(s), or in both; penes always present, sometimes with cuticular sheath ..... ***Styloscolex*** **[p. 470]**

23(22) Two pairs of testes, atria and male pores, in X and XI; two pairs of ovaries, in XII and XIII; spermathecae in XIV. Atria long tubular, can reach for 12 segments backwards. Penes in penial sacs covered with high glands. Spermathecal ampullae voluminous, penetrating one or two segments posteriad, ducts very short. Dorsal and ventral pharyngeal wall similarly developed. L = 23−25 mm ..... *Lamprortus orientalis* Rodriguez, 1994 [Korea]

23′ Testes, atria, and male pores usually two pairs, X–XI, spermathecae in XIII, respectively ..... ***Lamprodrilus*** [in part; **p. 469**]

Oligochaeta: Lumbriculida: Lumbriculidae: *Rhynchelmis*: Species (excluding Lake Baikal)

1 All or many chaetae with small or rudimentary upper tooth; spermathecae connected with esophagus 2

1′ All chaetae simple-pointed 4

2(1) Spermathecae two pairs, in VIII and IX 3

2′ Spermathecae one pair in IX; male pores in X, pore of unpaired, rudimentary atrium in IX; tentacle present or (in Lake Ohrid deeper zone) lacking; L ≤ 80 mm ..... *Rhynchelmis komareki* Hrabě, 1927 [Balkan Peninsula]

3(2) Dorsal and ventral chaetae with small upper tooth present but not always distinct; rudimentary atrium present in IX; L = 15−50 mm (Fig. 12.24(23, 24)) ..... *Rhynchelmis tetratheca* Michaelsen, 1920 [western Palaearctic]

3′ Dorsal chaetae with small upper tooth only; rudimentary atrium lacking; L = 50 mm ..... *Rhynchelmis granuensis onegensis* Hrabě, 1962 [Russia: Lake Onega]

4(1) Spermathecal pores only in VIII; rudimentary atrium in IX present or lacking 5

4′ Spermathecal pores in VIII and IX; no rudimentary atrium; color milky white in life; dorsolateral blood vessels in mid- and hindbody with 12 blind appendages; L = ∼50 mm ..... *Rhynchelmis granuensis granuensis* Hrabě, 1961 [central and southen Europe]

5(4) Rudimentary atrium in IX present 6

5′ Rudimentary atrium lacking 7

6(5) Worms 2−3 mm in diameter, red or bluish in life; mid- and hindbody segments with a pair of chloragogen-covered lateral blood vessels with many pulsating appendages; L = 80−140 mm (Fig. 12.24(21−22)) ..... *Rhynchelmis limosella* Hoffmeister, 1843 [western Palaearctic]

6′ Worms white in color; mid- and hindbody segments with a pair of chloragogen-covered lateral blood vessels with 1−3 pulsating appendages; L ≤ 65 mm; streams and alpine lakes ..... *Rhynchelmis vagensis* Hrabě, 1961 [Slovakia]

7(5) Red or pink in life; east Asian species 8

7′ Milky white in life; L = 50−60 mm; Carpathian alpine streams ..... *Rhynchelmis vejdovskyi* Hrabě & Černosvitov, 1926 [Ukraine]

8(7) Spermathecae with oval ampulla connected with esophagus; tubular atria covered with prostate glands in proximal third only; L = 29 mm ..... *Rhynchelmis malevici* (Sokolskaja, 1983) [northeastern Russia: Koryak Mountains]

8′ Spermathecae long, tubular, not connected with esophagus (unlike the congeners); atria entirely covered with prostate glands; L ≤ 110 mm ..... *Rhynchelmis orientalis* Yamaguchi, 1936 [Japan]

Oligochaeta: Lumbriculida: Lumbriculidae: *Stylodrilus*: Species (excluding Lake Baikal)

1 Spermathecae present in preatrial segment (mostly atria in X, spermathecae in IX) 2

1 Spermathecae lacking; atria in X, with pyriform very muscular ampulla and short duct; no penes; no dorsolateral blind vessels; chaetae with shorter upper tooth; L = 7−13 mm (Fig. 12.24(25, 26)) ..... *Stylodrilus sanguineus* Bretscher, 1900 [southern Europe]

2(1) Penes present; chaetae bifid with minute upper tooth 3

2′ Penes lacking; chaetae bifid or/and simple-pointed 6

3(2) Penes in X external 4

3′ Penes in X usually hidden in penial sac, sometimes protruded 6

4(3) Long, transparent external penes in directed posteriorad; L = 25−60 mm; freshwater (Fig. 12.24(27−31)) ..... *Stylodrilus heringianus* Claparède, 1862 [Holarctic. Sudan]

4′ Penes as conical protuberances; L = 15−18 mm ..... *Stylodrilus cernosvitovi* Hrabě, 1950 [Caspian Sea]

5(4) Large muscular bulb between atrium and penial sac; L = 13−20 mm (Fig. 12.24(32, 33)) ..... *Stylodrilus brachystylus* Hrabě, 1929 [Europe]

5′ Penial sac connected immediately with atrial duct; L = 6 mm (Fig. 12.24(34, 35)) ..... *Stylodrilus mollis* Timm, 1998 [Russia: Lake Taimyr in Siberia]

6(2) Chaetae (all or most) bifid, with minute upper tooth 7

6′ All chaetae simple-pointed 10

76) Secondary annulation beginning from IV or V 8

7′ Secondary annulation beginning from IX; some individuals with reproductive system shifted anteriorly 1−2 segments; L = 30 mm ..... *Stylodrilus opisthoannulatus* (Izosimov, 1962) [Russia: Lake Baikal, Angara and Enisej Rivers in Siberia]

8(7) All chaetae bifid 9

8′ II–III ventral chaetae simple-pointed; posterior segments with pair of dorsolateral blind blood vessels; forebody distinctly lighter than the brownish mid- and hindbody; L ≤ 36 mm on ..... *Stylodrilus leucocephalus* Hrabě, 1931 [Albania/Macedonia (Lake Ohrid)]

9(8) All chaetae bifid but the upper tooth distinctly visible only under high magnification; body wall epidermis glandular, mainly in the forebody and posteriormost part; L = ?; caves ..... *Stylodrilus mariae* Achurra & Erséus, 2015 [Spain]

9′ All chaetae distinctly bifid; body wall not glandular; no dorsolateral blind blood vessels; L = 10−15 mm; streams and deep lakes (Fig. 12.24(36−38)) ..... *Stylodrilus parvus* (Hrabě & Černosvitov, 1927) [Europe; Turkey; Caspian Sea]

10(6) Atria and male pores in X, spermathecae in IX 11

10′ Atria and male pores in XI, spermathecae in X; atria small, pyriform, wall glandular, proximally with multiple large, separate prostate glands; short ducts without penes; spermathecae with very long ampulla folded in X or partially reaching XI, and short duct; L ≥ 10 mm ..... *Stylodrilus suputensis* Timm, 1995 [southeastern Russia]

11(10) Ventral and dorsal chaetae uniform 12

11′ Ventral chaetae larger than dorsal ones, especially postclitellar segments, with distal half falciform; IX first pair testes and male funnels, much smaller; atria small, pyriform, with short duct, no penis; spermathecae in IX large, with short duct; L = 18−20 mm (Fig. 12.26(8−11)) ..... *Stylodrilus mirus* Čekanovskaja, 1956 [Russia: Enisej River in Siberia]

12(11) No transverse blood vessels in postclitellar segments 13

12′ Transverse blood vessels in postclitellar segments present (but not always studied) 14

13(12) Atria prolonged, reaching from X to XI, ampulla pyriform, transitioning into duct; conical penis in large muscular bulb protrusible; spermathecae in IX, ampulla with pyriform proximal and long, curved distal portion, transitioning into thick-walled duct of same length; L = 18−25 mm ..... *Stylodrilus curvithecatus* Collado, Martínez-Ansemil & Giani, 1993 [Spain]

13′ Atrial ampullae long oval, delimited to X, narrowing to duct, without penis; spermathecal ampullae pyriform, distinctly separated from duct; L = 12−22 mm; caves ..... *Stylodrilus sulci* (Hrabě, 1934)
[Bosnia and Herzegovina]

14(12) Atrial ampullae tubular, immediately ending with penis 15

14′ Atria consisting of pyriform or oval ampulla, and distinct duct 17

15(14) Atria delimited to X 16

15′ Atrial ampullae very long, over 2−4 segments; posterior body half, each segment with two pairs of simple or forked blind lateral vessels, without chloragogen; L = 20−30 mm (Fig. 12.24(39)) ..... *Stylodrilus subcarpathicus* Hrabě, 1929
[Ukraine: Carpathian Mountains]

16(15) Postclitellar dorsolateral blind blood vessels, two pairs per segment, with numerous long, irregular appendages; atria tubular, ending with distinct penis; L = 25−40 mm (Fig. 12.26(12−16)) ..... *Stylodrilus lemani* (Grube, 1879)
[Europe]

16′ Middle segments with two pairs, posterior segments with one pair of transverse vessels connecting the dorsal and ventral vessel; numerous blind appendages on lateral vessels and on dorsal vessel; L = ? ..... *Stylodrilus aurantiacus* (Pierantoni, 1904)
[Italy]

17(14) Atrial ampulla pyriform, duct long, protruding into XI 18

17′ Atrial duct short, limited to X 19

18(17) Conical penes in large sacs surrounded by gland cell layer; spermathecae in IX, ampullae suboval, long ducts well separated from ampullae and ending with a small conical tubercle surrounded by cavity similar to a penial sac; L = 23 mm ..... *Stylodrilus glandulosus* Giani & Martínez-Ansemil, 1984
[Spain]

18′ Atrial ampulla elongate, clavate, wall muscular, ducts thin and double-folded, ending with small conical penis; spermathecal ampullae large, sacculate, folded in IX or partially protruding into X; ducts shorter than ampulla; L = 21−32 mm ..... *Stylodrilus longiatriatus* Dembitsky, 1976
[Ukraine: Crimea]

19(17) Penes present 20

19′ Atria opening in male pore without penis; spermathecae with sacculate ampulla, length twice duct, duct narrow; pharyngeal glands present up to VI; L = ? ..... *Stylodrilus tschaunensis* Morev, 1982
[northeastern Russia]

20(19) Atrial ampullae elongate ovoid, ducts short with muscular walls; penes small conical, retractable; spermathecae in IX with large suboval ampulla and distinct, thick-walled duct; pharyngeal glands present to V; blood vessel system not studied; L = 17−25 mm ..... *Stylodrilus chukotensis* Sokolskaja, 1975
[Russia: Chukchi Peninsula]

20′ Atrial ampullae pyriform, ducts short; penes small conical; spermathecae with oval ampulla and distinct duct; pharyngeal glands present to VII (VIII); postclitellar lateral blood vessels with two pairs of simple or bifurcated blind appendages; L = ? (in vivo 35−50 mm) ..... *Stylodrilus absoloni* (Hrabě, 1970)
[central Europe]

Oligochaeta: Lumbriculida: Lumbriculidae: *Lumbriculus*: Species

1 All or most chaetae with shorter upper tooth 2

1′ All chaetae simple-pointed; spermathecae in XII, with very long ampulla and ventrolateral pore; L ≤ 25 mm (Fig. 12.24(3, 4)) *Lumbriculus illex* Timm & Rodriguez, 1994
[southeastern Russia]

2(1) Each atrium connected with one testis, male funnel and vas deferens, all located in same segment (prosoporous male ducts) 3

2′ Each functioning atrium receiving two vasa deferentia, one coming from anterior and second from same segment (semiprosoporous male ducts) 5

3(2) Asexual reproduction not known, may be rare; atrial duct straight, spermathecal pores ventral 4

3′ Asexual reproduction by architomy prevailing; sexually mature individuals rare, when present, the number and position of genitalia very variable, in most typical case one pair of atria in VIII and several pairs of spermathecae in postatrial segments; atrial duct making a zigzagged bend; spermathecal pores dorsolateral; L = 40−90 mm (but less in regenerating fragments); often cultivated (Fig. 12.24(40−44)) ..... *Lumbriculus variegatus* (Müller, 1774)
[Holarctic. Introduced elsewhere]

4(3) Testes, male funnels and atria two pairs, in VIII and IX, spermathecae in X and XI; atria short, erect; L = 32−39 mm ..... *Lumbriculus tetraporophorus* Popčenko, 1976
[Russia: Karelia]

4′ Testes, male funnels and atria commonly 3−4 pairs, in X–XII (XIII), spermathecae 4−5 pairs, in XIV–XIX; atria prolonged, bent posteriorly; L = 51−70 mm..... *Lumbriculus multiatriatus* Yamaguchi, 1937
[Japan]

5(2) One pair of atria 6

5′ Testes and functioning male funnels in VIII and IX; atria small erect, two pairs, in VIII and IX; only the second pair (in IX) connected with two pairs of vasa deferentia, thus servicing both pairs of testes while the male funnels in VII with vasa deferentia and atria in VIII (plesioporous male ducts), although fully developed, have no function; spermathecae four pairs, in X–XIII, with ventral pores; L = 23 mm ..... *Lumbriculus kolymensis* Morev, 1982
[northeastern Russia]

6(5) Atria erect or bent, the duct not zigzagged 7

6′ Atria elongate, with zig zagged bent duct near the male pore in XI; spermathecae with dorsolateral pores in XIII; sometimes an additional, unpaired spermatheca in XII or XIV; L = 15−17 mm .....*Lumbriculus sachalinicus* Sokolskaja, 1967
[Russia: Sahalin Island]

7(6) Spermathecal pores ventral or ventrolateral 8

7′ Spermathecal pores dorsolateral..... 9

8(7) Atria in X, long cylindrical, one of them reaching to XI. Two pairs of spermathecae with ventrolateral pores in XI and XII, those of the first pair smaller. L = 14 mm ..... *Lumbriculus olgae* Sokolskaja, 1976
[Russia: Chukchi Peninsula]

8′ Atria in XI (seldom in IX or X), elongate. Spermathecae with ventral pores in XIII–XVII (XVIII); L = 42−93 mm ..... *Lumbriculus japonicus* Yamaguchi, 1936
[Japan]

9(8) Atria mostly in XII (or IX, or XI), spermathecae two pairs, with pores in XIV and XV; L = 28−45 mm .....*Lumbriculus mukoensis* Yamaguchi, 1953
[Japan]

9′ Atria in X, clavate, erect; spermathecae several pairs in X–XIII, unpaired spermathecae may occur also in IX and XIV; L = 40−43 mm.....*Lumbriculus alexandrovi* Popchenko, 1976
[Russia: Karelia]

Oligochaeta: Lumbriculida: Lumbriculidae: *Trichodrilus*: Species

1 All or most chaetae bifid with shorter upper tooth..... 2

1′ All chaetae simple-pointed (seldom lacking) 5

2(1) Chaetae uniformly bifid in all segments 3

2′ Chaetae bluntly simple-pointed in II−IV, bifid from V on; II–IV with ventral chaetae considerably longer and thicker than dorsal; posterior chaetae all similar; L = ? (Fig. 12.25(7−11, 16))..... *Trichodrilus diversisetosus* Rodriguez & Giani, 1986
[France, Spain]

3(2) Forebody not flattened; no alate folds in genital region..... 4

3′ Forebody flattened, with deep median furrow, particularly in genital region, forming two ventrolateral alate folds; L = ∼10 mm (Fig. 12.25(12, 13, 17)) ..... *Trichodrilus strandi* Hrabě, 1936
[southern and central Europe]

4(3) Atria consisting of pyriform ampulla and indistinct duct, without penis; spermathecae consisting of large sacculate ampulla extending from X into XI, and long, distally dilated duct; L = 8−10 mm (Fig. 12.25(18))..... *Trichodrilus campoyi* Rodriguez, 1988
[France, Spain]

4′ Atria consisting of large suboval ampulla and long duct, ending with penis; spermathecae with oval ampulla and short duct; atria usually in IX and spermathecae in X but in some individuals genital system may be shifted forward one segment; L = 12−14 mm (Fig. 12.25(19)) ..... *Trichodrilus isabellae* Popčenko, 1988
[Russia: Ural Mountains]

5(1) Spermathecae 1−2 pairs, always only in postatrial segments (X or XI and/or XII)..... 6

5′ The first or single pair of spermathecae in atrial segment X; long, tubular atria filling X–XII, with one male pore in X and another in XI; female pores near 10/11; L = ?; caves (probably a single abnormal specimen)..... *Trichodrilus spelaeus* Moszyński, 1936
[Poland]

6(5) Atria and male pores in X..... 7

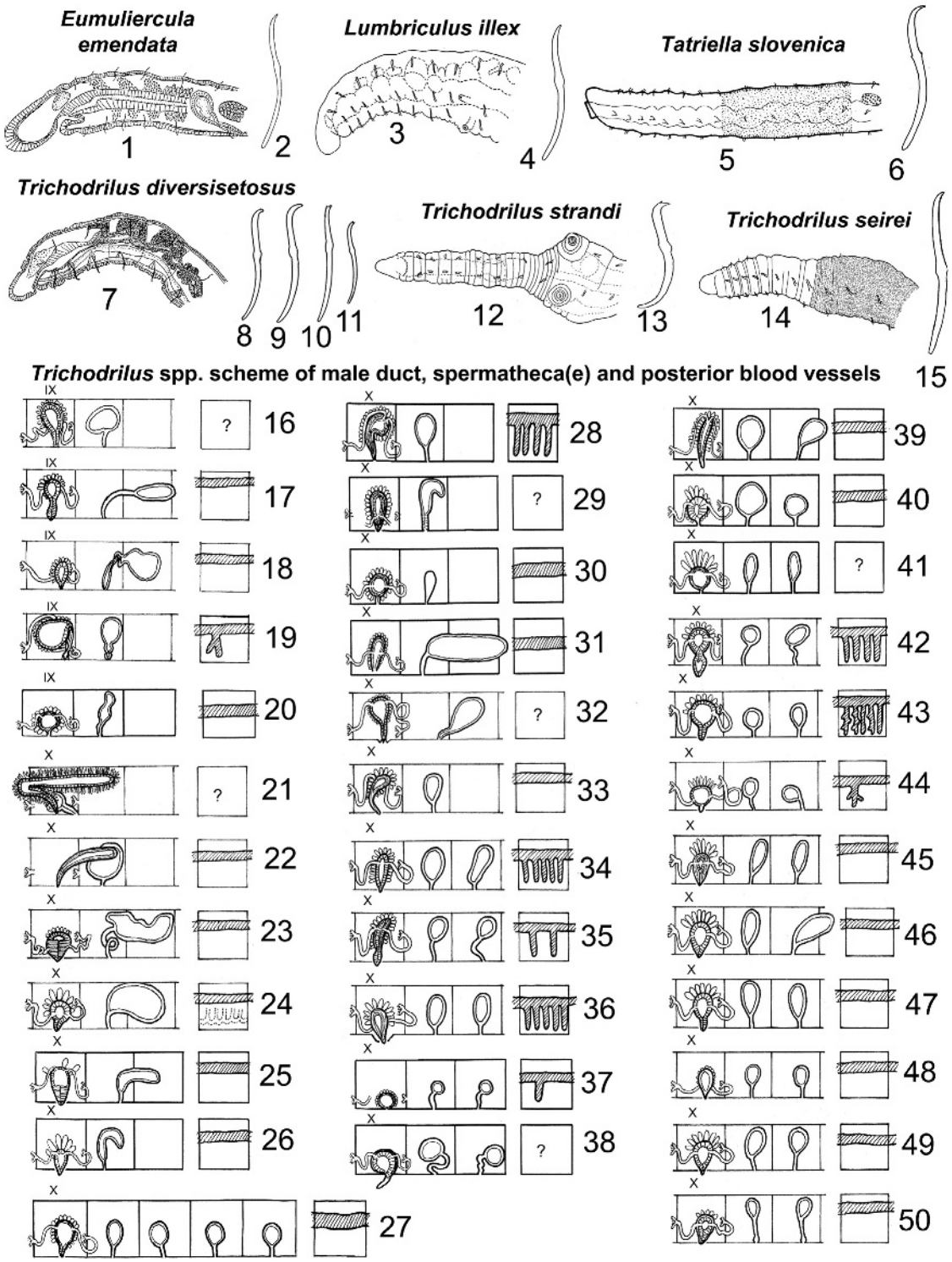


FIGURE 12.25 Lumbriculidae II: (1, 2): *Eumuliercula emendata*: (1) forebody of sexually mature specimen with spermatheca, (2) chaeta; (3, 4): *Lumbriculus illex:* (3): forebody of sexually mature specimen with male pore, (4) chaeta; (5, 6): *Tatriella slovenica*: (5) forebody of sexually mature specimen with clitellum, (6) chaeta; (7–11): *Trichodrilus diversisetosus*: (7) forebody, (8–10): anterior ventral chaetae, (11) posterior chaeta; (12, 13) *Trichodrilus strandi*: (12) forebody of sexually mature specimen with male pores, (13) chaeta; (14, 15) *Trichodrilus seirei*: (14) forebody of sexually mature specimen with clitellum, (15) chaeta; (16–50): *Trichodrilus* spp., scheme of male duct (located in IX or X, in separate species), spermatheca(e) and posterior dorsal vessel bearing or devoid of blind lateral vessels: (16) *T. diversisetosus*, (17) *T. strandi*, (18) *T. campoyi*, (19) *T. isabellae*, (20) *T. metohiensis*, (21) *T. spelaeus*, (22) *T. cernosvitovi*, (23) *T. bonheurensis*, (24) *T. pragensis*, (25) *T. sketi*, (26) *T. macedonicus*, (27) *T. rouchi*, (28) *T. ptujensis*, (29) *T. itchaensis*, (30) *T. drimi*, (31) *T. stammeri*, (32) *T. gordeevi*, (33) *T. tatrensis*, (34) *T. intermedius*, (35) *T. leruthi*, (36) *T. macroporophorus*, (37) *T. capilliformis*, (38) *T. longipenis*, (39) *T. tacensis*, (40) *T. angelieri*, (41) *T. montenegrinus*, (42) *T. cantabrigiensis*, (43) *T. allobrogum*, (44) *T. aporophorus,* (45) *T. claparedei*, (46) *T. medius*, (47) *T. tenuis*, (48) *T. seirei*, (49) *T. hrabei*, (50) *T. moravicus*.

6′ Atria and male pores in IX; penes lacking; spermathecae with pores in X, large tubular ampullae filling X and XI; L = 36 mm; groundwater (Fig. 12.25(20)) ..... *Trichodrilus metohiensis* Karaman, 1986 [Kosovo]

7(6) Spermathecae 1−2 pairs 8

7′ Spermathecae four pairs, in XI–XIV, with globular ampulla; L = ?; groundwater (Fig. 12.25(27)) ..... *Trichodrilus rouchi* Rodriguez & Giani, 1994 [Spain]

8(7) Spermathecae one pair, in XI 9

8′ Spermathecae two pairs, in XI and XI 19

9(8) Atrial ampullae pyriform or oval, not penetrating into XI 10

9′ Atria tubular, length ∼10 times width, not distinctly divided into ampulla and duct, penetrating from X into XI; L = ? (Fig. 12.25(22)) ..... *Trichodrilus cernosvitovi* Hrabě, 1938 [Europe]

10(9) Atria pyriform, without separate duct, distal portion narrowing, inner epithelium thick, forming conical pseudopenis; spermathecae with distinct duct and very large sacculate ampulla penetrating into XII 11

10′ Atria with or without duct but ampullae wall uniform 12

11(10) Spermathecal ducts long; pharyngeal glands poorly developed in III–V; L = ? (Fig. 12.25(23)) ..... *Trichodrilus bonheurensis* Giani & Rodriguez, 1994 [France]

11′ Spermathecal ducts much shorter than ampullae; pharyngeal glands present up to VII; L ≤ 32 mm; groundwater (Fig. 12.25(25)) ..... *Trichodrilus sketi* Hrabě, 1963 [Slovenia]

12(10) Atria consisting of ampulla and duct 13

12′ Atrial ampullae walls thick and muscular, with phallic end without duct; spermathecae with long tubular ampulla and shorter, discrete duct; L = 16−24 mm; groundwater (Fig. 12.25(26)) ..... *Trichodrilus macedonicus* Karaman, 1986 [Macedonia]

13(12) Atrial ducts at least as long as the ampullae, both heavy muscular 14

13′ Atrial ducts shorter than ampullae 15

14(13) Hindbody with dorsolateral blind blood vessels, four pairs per segment; L = 18.5 mm; groundwater (Fig. 12.25(28)) ..... *Trichodrilus ptujensis* Hrabě, 1963 [Slovenia]

14′ No dorsolateral blind blood vessels; L = ∼10 mm (Fig. 12.25(33)) ..... *Trichodrilus tatrensis* Hrabě, 1937 [Germany; Slovakia]

15(13) Atrial wall with thin muscle layer 16

15′ Atrial wall heavily muscular 17

16(15) Atrial ampullae suboval or pyriform, vasa deferentia entering medially; hindbody dorsolateral blind blood vessels 4−6 per segment; L = 22−40 mm (Fig. 12.25(24)) ..... *Trichodrilus pragensis* Vejdovský, 1876 [Europe]

16′ Atrial ampullae pyriform, vasa deferentia entering proximally; dorsolateral blind vessels not observed; L = 10−14 mm (Fig. 12.25(32)) ..... *Trichodrilus gordeevi* Popčenko, 1978 [Russia: Kola Peninsula]

17(15) Atrial ducts not muscular, penes not observed 18

17′ Both atrial ampullae and ducts heavily muscular; penes in penial sacs; spermathecal duct walls thick; L = 20 m (Fig. 12.25(29)) ..... *Trichodrilus itchaensis* Sokolskaja, 1973 [Russia: Kamchatka]

18(17) Atrial ampullae spherical; spermathecae clavate; L = 32 mm; groundwater (Fig. 12.25(30)) ..... *Trichodrilus drimi* Karaman, 1986 [Kosovo]

18′ Atrial ampullae elongate; spermathecae large, with sacculate ampulla protruding from XI into XII; L = ?; groundwater (Fig. 12.25(31)) ..... *Trichodrilus stammeri* Hrabě, 1937 [Italy; Slovenia]

19(8) All chaetae with distal or medial nodulus 20

19′ Chaetae with proximal nodulus, in postclitellar dorsal bundles thinner but with obtuse tip; atria consisting of a spherical ampulla without duct or penis; L = ?; groundwater (Fig. 12.25(37)) ..... *Trichodrilus capilliformis* Rodriguez & Giani, 1994 [Spain]

20(19) No external penes 21

20′ Atria spherical, muscular, without duct, ending with long external pseudopenes consisting of atrial inner epithelium; L = ?; groundwater (Fig. 12.25(38)) ..... *Trichodrilus longipenis* Rodriguez & Giani, 1994 [Spain]

21(20) Atrial ampullae short tubular; no atrial ducts, penes present 22

21′ Atrial ampullae pyriform or spherical, ducts present or lacking 24

22(21) Penes small 23

22′ Penes large, bulbous, atrial ampulla length ~two times penes; posterior transverse vessels 1−3 pairs per segment; groundwater (Fig. 12.25(35)) ..... *Trichodrilus leruthi* Hrabě, 1939 [Belgium]

23(22) 2−6 pairs of dorsolateral blind blood vessels per segment; L = 30−60 mm (Fig. 12.25(34)) ..... *Trichodrilus intermedius* (Fauvel, 1903) [France]

23′ No dorsolateral blind blood vessels; X ventral posterior portion invaginated, male pores on invagination edge; L = 13−21 mm; groundwater (Fig. 12.25(39)) ..... *Trichodrilus tacensis* Hrabě, 1963 [Slovenia]

24(21) No dorsal glandular pads 25

24′ Each posterior segment dorsally with a pad of thickened, glandular epithelium; no dorsolateral blind blood vessels; atria with pyriform ampulla and small duct opening on porophore; L = 14 mm; groundwater (Fig. 12.25(40)) ..... *Trichodrilus angelieri* Giani & Rodriguez, 1994 [southwestern Europe]

25(24) No large penial sacs 26

25′ Atria a suboval ampulla with small penis in large penial sac; the latter length subequal to ampulla; hindbody dorsolateral blind blood vessels simple, 3−5 per segment; L = ?; groundwater (Fig. 12.25(42)) ..... *Trichodrilus cantabrigiensis* (Beddard, 1908) [United Kingdom]

26(25) Dorsolateral blind blood vessels present in posterior segments 27

26′ Dorsolateral blind blood vessels lacking 29

27(26) No large porophores 28

27′ Atria pyriform, with very thick muscular layer, ectal portion protruding above body surface inside large protuberances terminating with small penes; posterior segments each with several pairs of simple transverse vessels; L = 18−20 mm; groundwater (Fig. 12.25(36)) ..... *Trichodrilus macroporophorus* Hrabě, 1954 [Austria, Germany]

28(27) Atrial ampullae spherical, thick-walled, with penis in penial sac, without duct; each posterior segment with several pairs of blind, distally forked dorsolateral blood vessels; L = 8−13 mm (Fig. 12.25(44)) ..... *Trichodrilus aporophorus* Popčenko, 1976 [Russia: Karelia]

28′ Atrial ampullae pyriform, efferent duct indistinct, short; penes small; posterior dorsolateral blind blood vessels simple or with small appendages, 3−6 pairs per segment; L = 12−15 mm (Fig. 12.25(43)) ..... *Trichodrilus allobrogum* Claparède, 1862 [Europe]

29(26) Atrial ampullae ovoid or suboval, bearing high prostate cells proximally only, duct short; posterior blood vessels not studied 30

29′ Atria pyriform, without distinct duct; no dorsoventral blind blood vessels 31

30(29) Atrial ampullae ovoid, duct very short ending with minute porophore; pharyngeal glands reaching to VI; posterior blood vessels not studied; L ≥ 4 mm; groundwater (Fig. 12.25(47)) ..... *Trichodrilus tenuis* Hrabě, 1960 [Europe; Morocco]

30′ Atrial ampullae small suboval, with many multicellular prostate glands longer than ampulla; short atrial ducts opening in male pores without penis; L = ? (Fig. 12.25(41)) ..... *Trichodrilus montenegrinus* Karaman, 1973 [Albania/Montenegro: Lake Skadar]

31(29) Atria with not very thick (<15 μm) muscular layer 32

31′ Atria with very thick (>20 μm) muscular layer and small penis; pharyngeal glands reaching VIII; spermathecae with long ampulla and short duct; L = 30 mm (Fig. 12.25(45)) ..... *Trichodrilus claparedei* Hrabě, 1938 [France]

32(31) Atria not compressed 33

32′ Atria laterally compressed, ovoid, terminating in small protrusible penis; prostate glands high; pharyngeal glands to VII; L = 8−15 mm (Fig. 12.25(49)) ..... *Trichodrilus hrabei* Cook, 1967 [United Kingdom]

33(32) No transverse furrow on prostomium 34

33′ Prostomium dorsally with transverse furrow; pyriform atria with thick inner epithelium, without duct, terminating in small penis; pharyngeal glands reaching VI; L = 17−18 mm; groundwater (Fig. 12.25(46)) ..... *Trichodrilus medius* Hrabě, 1960 [Germany]

34(33) Pharyngeal glands reaching VI or VII; duct shorter than ampulla 35

34′ Pharyngeal glands reaching VIII; spermathecae ampulla ovoid, duct long and slightly dilating at external pore; L = 10−30 mm (Fig. 12.25(50)) ..... *Trichodrilus moravicus* Hrabě, 1937 [central Europe]

35(34) Pharyngeal glands reaching VI; spermathecal ducts shorter than ampulla; L = 4−10 mm (Fig. 12.25(14, 15, 48)) ..... *Trichodrilus seirei* Timm, 1979 [Estonia]

35′ Pharyngeal glands reaching VII; the first pair of spermathecae smaller than the second; L = ?; brackish water ..... *Trichodrilus pauper* Finogenova, 1973 [Caspian Sea]

Oligochaeta: Lumbriculida: Lumbriculidae: *Eumuliercula*: Species

1 Ovaries in VII and VIII, functioning female funnels and pores in 7/8 and 8/9, additional single or rudimentary female funnels can occur in 6/7 and 9/10; paired spermathecae in VII and VIII, an additional, unpaired spermatheca once observed on one side of VI; L = ? ..... *Eumuliercula casta* (Timm, 1995) [southeastern Russia]

1′ Ovaries in VIII and IX, female funnels and pores in 8/9 and 9/10, spermathecae with pores in VII and X; L ≥ 10 mm (Fig. 12.25(1, 2)) ..... *Eumuliercula emendata* (Timm, 1995) [southeastern Russia]

Oligochaeta: Lumbriculida: Lumbriculidae: *Tatriella*: Species

1 Atrial ampulla oval, confined to X; prostate cells attached to the junction of atrial ampulla and efferent duct only, or lacking; no blind blood vessels in hindbody; L = 8−28 mm (Fig. 12.25(5, 6)) ..... *Tatriella slovenica* Hrabě, 1939 [Holarctic]

1′ Atrial ampulla prolonged, reaching posteriorly to XII, covered with prostate cells; spermathecal ampulla spherical; dorsolateral blind blood vessels present in hindbody; L = 10−18 mm ..... *Tatriella longiatriata* Popčenko, 1976 [Russia: Karelia]

Oligochaeta: Lumbriculida: Lumbriculidae: *Cookidrilus*: Species

1 Spermathecae three pairs, in X–XII; atrial ampullae covered with prostate glands; penes lacking; L = ?; groundwater ..... *Cookidrilus speluncaeus* Rodriguez & Giani, 1987 [France]

1′ Spermathecae two pairs, in X and XI; atrial ampullae with prostate glands on apex only, ducts ending with protrusible penis; L = 15 mm; groundwater ..... *Cookidrilus ruffoi* Giani, Martínez-Ansemil & Sambugar, 2004 [France]

Oligochaeta: Lumbriculida: Lumbriculidae: *Pseudorhynchelmis*: Species (excluding Lake Baikal)

1 Ventral chaetae very thick in fore- and midbody from IV; L = 35−40 mm (Fig. 12.26(1−7)) ..... *Pseudorhynchelmis paraolchonensis* Giani & Martínez-Ansemil, 1984 [France]

1′ No thickened ventral chaetae; X male pores with modified ventral chaetae with slightly proximal nodulus, distally straight, surrounded with small copulatory glands; L = 12.5−16 mm ..... *Pseudorhynchelmis parva* (Michaelsen, 1905) [Russia: Lake Baikal and Angara River in Siberia]

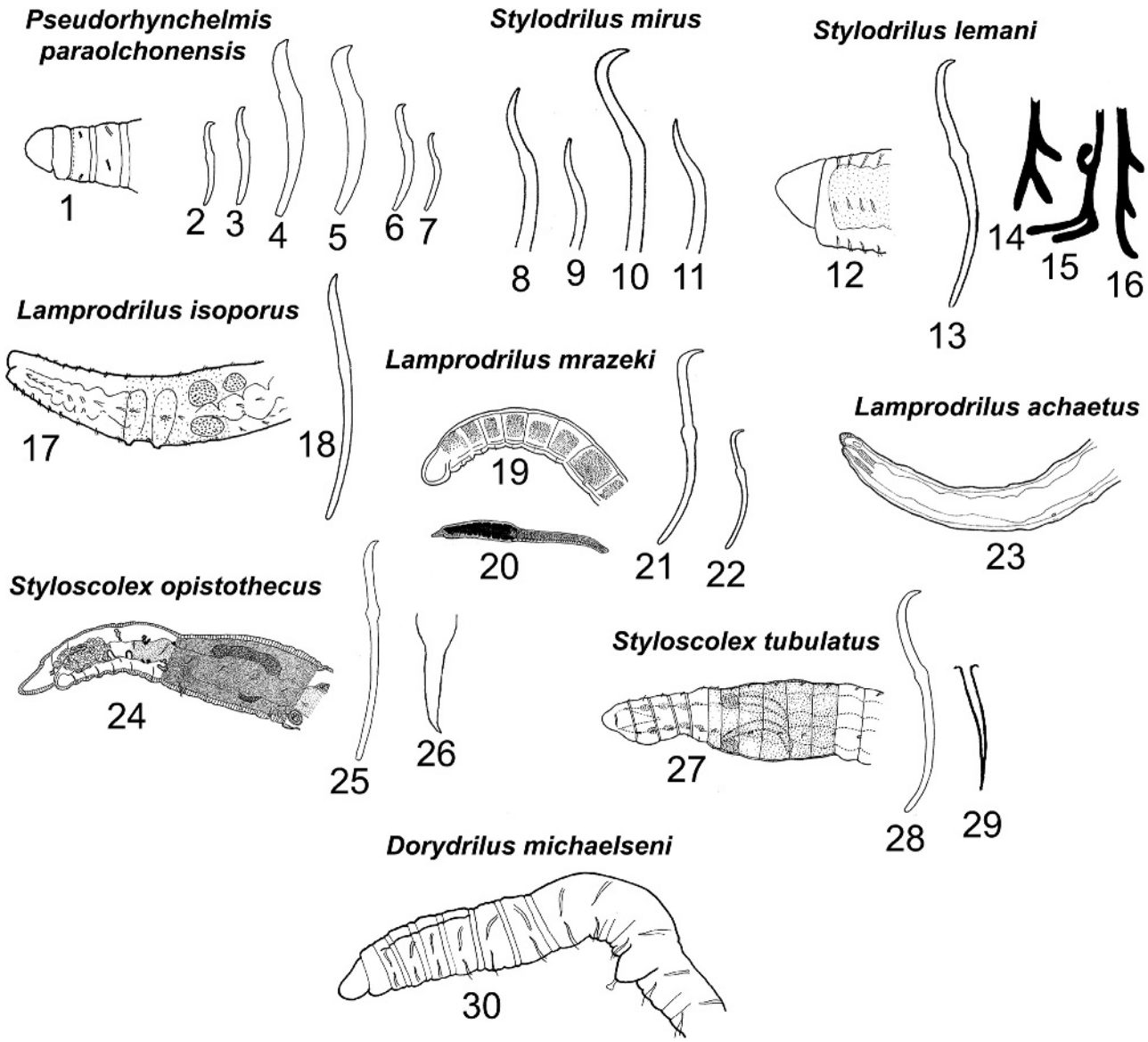


FIGURE 12.26 Lumbriculidae III and Dorydrilidae: (1–7): *Pseudorhynchelmis paraolchonensis*: (1) anterior end, (2–7): sequential chaetae from anterior end, midbody, and posterior region; (8–11): *Stylodrilus mirus*: (8) anterior ventral chaeta, (9) anterior dorsal chaeta, (10) posterior ventral chaeta, (11) posterior dorsal chaeta; (12–16): *Stylodrilus lemani*: (12) anterior end, (13) chaeta, (14–16): blind transversal vessels from hind body; (17, 18): *Lamprodrilus isoporus*: (17) forebody of mature specimen with clitellum, (18) chaeta; (19–22): *Lamprodrilus mrazeki*; (19) forebody, (20) young specimen from cyst, with regenerating ends, (21) ventral chaeta, (22) dorsal chaeta; (23) *Lamprodrilus achaetus*, forebody of mature specimen; (24–26): *Styloscolex opistothecus*: (24) forebody of mature specimen with clitellum, (25) chaeta, (26) penis sheath; (27–29): *Styloscolex tubulatus*: (27) forebody of mature specimen with clitellum, (28) chaeta, (29) penis sheath; (30) *Dorydrilus michaelseni*, forebody of mature specimen with protruded penis.

Oligochaeta: Lumbriculida: Lumbriculidae: *Lamprodrilus*: Species (excluding Lake Baikal)

1 Chaetae present in all segments beginning from II 2

2′ Chaetae lacking in some body regions or completely; general appearance nematode-like, without external intersegmental furrows; atria and male pores in X and XI on conical protuberances, spermathecal pores in XIII; L = 9−12 mm (Fig. 12.26(23)) ..... *Lamprodrilus achaetus* Izosimov, 1962
[Russia: Lake Baikal and Karelia; Finland]

2(1) No asexual reproduction, no encysting 3

2′ Asexual reproduction by architomy (fragmentation) prevailing, regenerates common at both ends; mature animals with 1−2 pairs of atria and male pores between VI–IX, most often in VIII; 1−3 pairs of spermathecal pores for two segments caudad, between VIII–XIII, most often in X; two pairs of dark chloragogen transversal vessels, with blind appendages, per segment beginning from VI–VIII; anterior ventral chaetae bigger than dorsal; L = 25−40 mm; temporary pools, encysting in drought, fragmenting in cysts (Fig. 12.26(19−22)) ..... *Lamprodrilus mrazeki* Hrabě, 1929
[central Europe]

3(2) Atria and male pores one pair, in X 4

3′ Atria and male pores two pairs, in X and XI, or one pair in VII, VIII, or IX; no copulatory glands; spermathecae with large ampulla reaching up to XIV–XV; anterior chaetae thinner and more curved; L = 21−27 mm ..... *Lamprodrilus intermedius* Hrabě, 1931
[Albania/Montenegro: Lake Ohrid; Russia: Karelia (?)]

4(3) Atria and male pores always two pairs, in X and XI; distal part of atrial ducts penetrating glandular-muscular bulbs; no copulatory glands 5

4′ Atria and male pores three to four pairs, in VIII–XI or IX–XI; atria short tubular, conical penes in sacs with small penial bulbs; large copulatory glands in the segments following those with male pores; every gland opening on a muscular, phalliform papilla sitting in a respective sac; spermathecae variable, one to five pairs, with small suboval ampulla and thick muscular duct ending with muscular papilla; L = 40−115 mm ..... *Lamprodrilus satyriscus* Michaelsen, 1901
[Russia: Lake Baikal and Enisej River in Siberia]

5(4) Atrial ampulla tubular, duct short 6

5′ Atria fusiform, without duct; atria of first pair smaller; small conical penes surrounded with massive muscular bulbs; spermathecae in XIV, ampullae ovoid, ducts with pores in 13/14 ..... *Lamprodrilus isossimovi* Morev, 1982
[northeastern Russia]

6(5) Postclitellar transverse blood vessels branched 7

6′ Postclitellar transverse blood vessels simple or lacking 8

7(6) Postclitellar segments with two pairs of richly branched transversal vessels per segment; atrial ducts surrounded by large glandular-muscular bulbs; penes short conical, in wide but shallow penial sacs; spermathecae in XIII, with globular ampulla and long duct; L = 15−22 mm ..... *Lamprodrilus jamburaensis* Hrabě, 1980
[Russia: western Siberia]

7′ In first postclitellar segments one pair simple transversal vessels, from XX two pairs and with appendages; atrial ducts short, conical penes in muscular penial sacs; spermathecae in XIII, with oval ampulla and equally long duct; L ≥ 18 mm ..... *Lamprodrilus michaelseni* Hrabě, 1929
[Macedonia]

8(6) Penes with penial sacs present 9

8′ No penial sacs but atrial ducts opening in muscular penial bulbs 11

9(8) Chaetae uniform. Atrial ampullae covered with prostate cells along their very length. Spermathecal ampullae long sacculate, reaching XIV, suddenly separated from the narrow ducts 10

9′ Anterior chaetae thinner and more curved than the rest; hindbody without transversal vessels or appendages on dorsal vessel; atrial ampullae only proximally with prostate cells; spermathecal ampullae oval, may reach into XIV; duct longer than ampulla; some individuals with extra spermatheca in XIV; L = 13−20 mm ..... *Lamprodrilus ochridanus* Hrabě, 1931
[Albania/Macedonia: Lake Ohrid]

10(9) Transversal blood vessels lacking in hindbody but short blind appendages can occur at dorsal vessel; rarely a third, unpaired spermatheca occurs, with pore in XIV; L = 9−21 mm (to 20−40 mm in Lake Baikal) (Fig. 12.26(17, 18)) ..... *Lamprodrilus isoporus* Michaelsen, 1901
[northern Europe; Lake Baikal; Lake Taimyr in northern Siberia]

10′ Hindbody dorsal blood vessel without transversal vessels or appendages; L = 9−20 mm ..... *Lamprodrilus pygmaeus* Michaelsen, 1901
[Russia: Lake Baikal; eastern Siberia; Karelia (introduced)]

11(8) Intersegmental furrows inconspicuous or lacking, cuticle thick, iridescent; body externally nematode-like; blind transversal vessels present in hindbody; L = 30−42 mm ..... *Lamprodrilus wagneri* Michaelsen, 1901
[Russia: Lake Baikal, Angara and Enisej Rivers]

11′ Intersegmental furrows conspicuous; first pair of atria, in X, smaller; dorsolateral blind vessels in mid- and hindbody at least two per segment, simple or hardly branched; L = 17−30 mm ..... *Lamprodrilus tolli* Michaelsen, 1901 [northeastern Russia]

Oligochaeta: Lumbriculida: Lumbriculidae: *Styloscolex*: Species (excluding Lake Baikal)

1 Ovaries in the segment immediately following the testicular/atrial segment; usually no penial sheaths (subgenus *Neoscolex*) 2

1′ A "sterile" segment present between the testicular segment VIII, and the ovarial segment X; penial sheaths present (subgenus *Styloscolex*) 5

2(1) One pair of testes, atria, and male pores 3

2′ Testes, atria, and male pores two pairs, in VIII and IX, spermathecae with pores in VII and VIII; atria long tubular, proximal ends may reach posteriorly for two segments, covered with prostate cells; penes long conical without sheath but in thick-walled penial sacs, opening on small porophores; L = ? ..... *Styloscolex* (*Neoscolex*) *distinctus* Morev, 1984 [northeastern Russia]

3(2) Testes, atria, and male pores in VIII 4

3′ Testes, atria, and male pores in VII, spermathecal pores in VI; atria large sacciform, with thick muscular walls and thin prostate cover consisting of single cells, may reach VIII; thin penes in muscular penial sacs without penial sheath; L = 30−60 mm ..... *Styloscolex* (*Neoscolex*) *sokolskajae* Morev, 1978 [northeastern Russia]

4(3) Spermathecae two pairs in VI and VII; atria long sacculate, narrowing distally, thin-walled, prostate cover thin; penes short, massive, without sheath; L = ? ..... *Styloscolex* (*Neoscolex*) *macer* Sokolskaja, 1976 [Russia: Chukchi Peninsula]

4′ Spermathecae in VII; atria cylindrical and very long, reaching from VIII backwards to XII, with thick muscular walls covered with thin layer of prostate cells; penes in long, distally very narrow cuticular sheaths; L ≤ 20 mm ..... *Styloscolex* (*Neoscolex*) *levanidovi* Sokolskaja, 1977 [Russia: Chukchi Peninsula]

5(1) Spermathecae only either before, or after the atrial segment 6

5′ Spermathecae two pairs, in VII and XI; atria long tubular, thick-walled, proximal end reaching X; male pore in VIII; penes long, with cuticular sheath; L = 25 mm ..... *Styloscolex tetrathecus* Burow, 1931 [Russia; China; Japan]

6(5) Spermathecae before atrial segment, with pores in VII 7

6′ Spermathecae after atrial segment, with pores in XI or in X and XI 9

7(6) Penes tubular; spermathecal ampullae not directed in opposite directions 8

7′ Penes short, conical; tubular atria reaching from VIII to XI; spermathecae with pores in VII but ampullae reaching neighboring segments, directed oppositely; L = 18−20 mm ..... *Styloscolex asymmetricus* Izosimov, 1962 [Russia: Lake Baikal and Angara River]

8(7) Atria tubular, proximal end reaching IX; penial sacs in VIII, with bulbous proximal and tubular distal portion; proximal portion with doubly folded channel with thin penis in chitinous penial sheath; channel lined with similar chitinous layer; spermathecae in VII, with sacculate ampulla gradually transiting into much thinner duct; L = 13.5 mm ..... *Styloscolex hankensis* Timm & Všivkova, 2009 [Russia/China: Lake Hanka]

8′ Atria elongated fusiform, proximal end reaching posteriorly into IX or X, distal end forming a narrow duct ending with tubular, muscular penial sac; penes long, distally narrowing, covered with thickened cuticle; large glands attached from inside to papilla bearing male pore; spermathecae in VII relatively large, with tubular folded ampulla and thick-walled duct; L = 20−30 mm ..... *Styloscolex japonicus* Yamaguchi, 1937 [Japan]

9(6) Spermathecae one pair with pores and short ducts in XI, long ampullae in XII–XIII (XIV); atrial ampullae reaching from VIII into next segment; penes long conical, with cuticular sheath, in muscular penial sac; L ≥ 25 mm (Fig. 12.26(24−26)) ..... *Styloscolex opisthothecus* Sokolskaja, 1969 [Russia: Kamchatka Peninsula. Nearctic]

9′ Spermathecae two pairs, in X and XI, with irregular sacculate ampulla often protruding into opposite side or neighboring segment; duct clearly shorter than ampulla; atrial ampullae reaching posteriorly to X or XI; long penial sacs surrounded by massive copulatory gland; tubular penes long and stiff, distally tapering, lined with thick cuticle both from outside and inside; L = 14−27 mm (Fig. 12.26(27−29)) ..... *Styloscolex tubulatus* Timm, 1994 [northeastern Russia]

Oligochaeta: Lumbriculida: Lumbriculidae: Genera (Lake Baikal)

Modified after Semernoy (2004).

1 Chaetae bifid, with shorter upper tooth 2

1′ Chaetae simple-pointed (but can be lacking in one species) 4

2(1) Reproduction only sexual 3

2′ Reproduction mainly by architomy (fragmentation); number and location of reproductive organs, if present, variable; anterior end with brown pigment in body wall; L = 40–90 mm; bays and isolated lagoons (Fig. 12.24(40–44)) ..... *Lumbriculus variegatus* (Müller, 1774)
[Holarctic. Introduced elsewhere]

3(2) Two pairs of testes and atria, in X and XI, with male pores in 10/11 and 11/12; spermathecae in XIII and XIV, clitellum in X–XIV; no penes; L = 30 mm ..... *Wsewolodus mixtus* Semernoy, 2004
[Lake Baikal]

3′ Two pairs of testes in IX and X, single pair of mostly pyriform atria, and male pores in X, spermathecae in IX (but sometimes the reproductive system shifted forward by 1–2 segments); penes present or lacking ..... ***Stylodrilus*** **[p. 471]**

4(1) Spermathecae after the gonadal segments 5

4′ Spermathecae before the gonadal segments 7

5(4) Usually single pairs of atria and male pores; if more atria, then two pairs of ovaria 6

5′ Atria and male pores in 2–5 pairs, always a single pair of ovaria ..... ***Lamprodrilus*** **[p. 474]**

6(5) Single pair of testes and atria in XI; atria long, reaching posterior end of XII, male pores with muscular penes in penial sacs; spermathecae in XIII; anteriormost 11 segments externally without noticeable intersegmental furrows; pharynx and esophagus as far as XI heavily muscular, with triangular lumen; L ≥ 80 mm ..... *Agriodrilus vermivorus* Michaelsen, 1905
[Lake Baikal]

6′ Atria in X, spermathecae in XII. Forebody not modified ..... ***Teleuscolex*** **[p. 476]**

7(4) Testes in IX and X, or only in X; male pores in X, atria covered with numerous clusters of prostate cells; no "sterile" segment; penes present or absent; prostomium with or without a small tentacle 8

7′ Testes and atria in VII or VIII, ovaria in IX or X (a "sterile" segment present between the testicular and ovarial segment); penes retractable into long, thin sheaths ..... ***Styloscolex*** **[p. 476]**

8(7) Large worms, IX with pair of rudimentary atria; one pair of testes and male funnels in X; two pairs of vasa deferentia, first pair rudimentary, without funnels; atria long, tubular, reaching XVII; male pores on small tubercles, without penial sacs; spermathecae in IX, with 2–3 diverticula, one connected with esophagus; prostomium with or without tiny tentacle; L ≤ 185 mm, diameter 4.5 mm (Fig. 12.27(29, 30)) ..... *Rhynchelmis brachycephala* Michaelsen, 1901
[Lake Baikal]

48′ Much smaller worms; no rudimentary atria, no tentacle; two pairs of testes and male funnels, in IX and X; small conical penes in penial sacs ..... ***Pseudorhynchelmis*** **[p. 477]**

Oligochaeta: Lumbriculida: Lumbriculidae: *Stylodrilus*: Species (Lake Baikal)

1 No penes; male pores on small tubercles only 2

1′ Penes present 7

2(1) Body wall very thick 3

2′ Body wall usual, thin 4

3(2) Secondary annulation beginning from IV–VII; L = 20 mm (Fig. 12.27(1, 2)) ..... *Stylodrilus sulcatus* (Semernoy, 2004)
[Lake Baikal]

3′ Secondary annulation beginning from VI; L ≤ 23 mm ..... *Stylodrilus crassus* (Izosimov, 1962)
[Lake Baikal]

4(2) Chaetae as common bifids, with undivided teeth 5

4′ At least some chaetae with branched upper tooth 6

5(4) Secondary annulation beginning from VI–VII; L = ~42 mm (Fig. 12.27(3, 4)) ..... *Stylodrilus asiaticus* (Michaelsen, 1901)
[Lake Baikal]

5′ Secondary annulation beginning from IX; some individuals with reproductive system shifted forward 1–2 segments; L = 30 mm ..... *Stylodrilus opisthoannulatus* (Izosimov, 1962)
[Lake Baikal, Angara and Enisej River in Siberia]

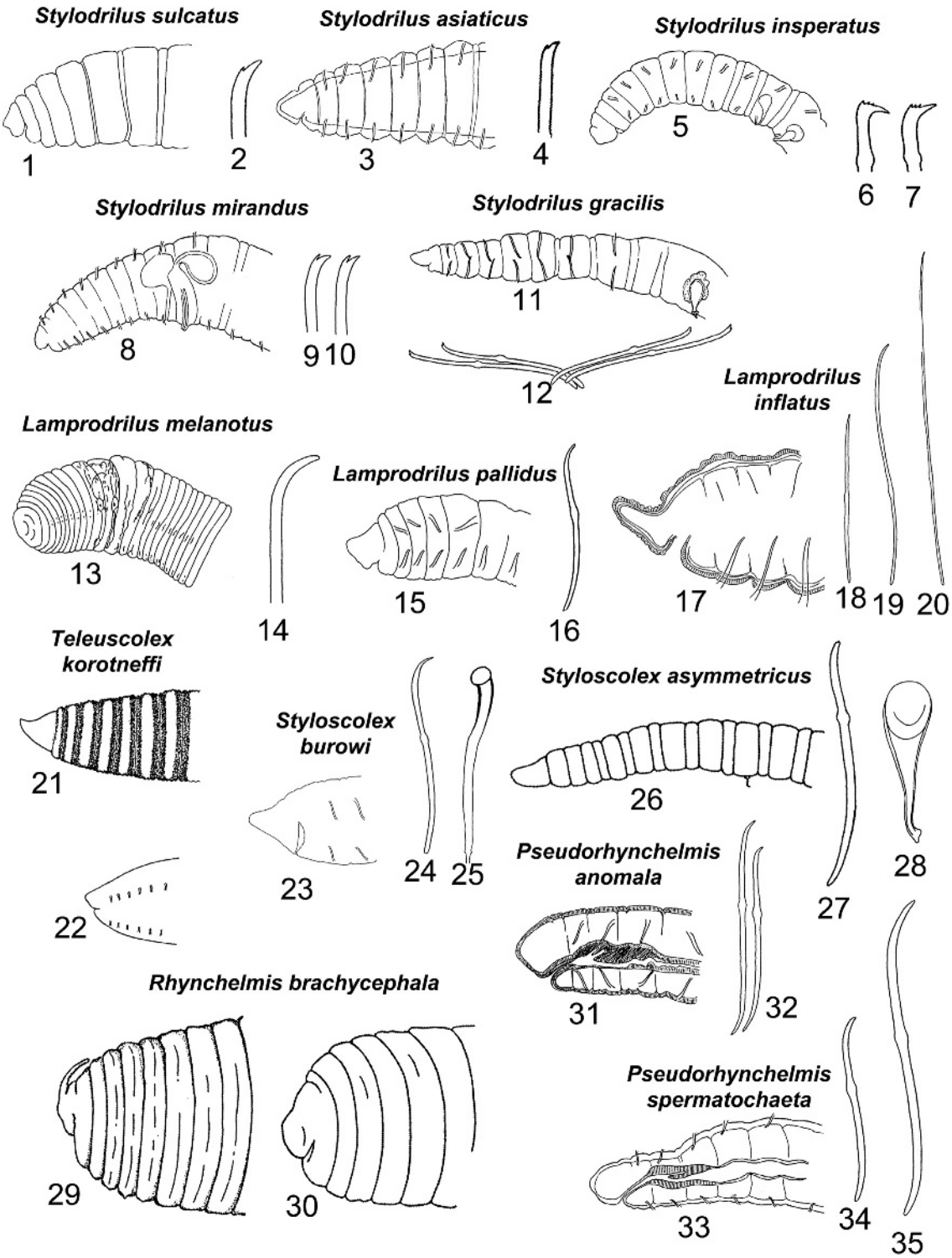


FIGURE 12.27 Lumbriculidae from Lake Baikal: (1, 2): *Stylodrilus sulcatus*: (1) anterior end, (2) chaeta; (3, 4): *Stylodrilus asiaticus*: (3): anterior end, (4) chaeta; (5–7): *Stylodrilus insperatus*: (5) forebody of sexually mature specimen, (6, 7) chaetae; (8–10): *Stylodrilus mirandus*: (8) forebody of sexually mature specimen, (9, 10) chaetae; (11, 12) *Stylodrilus gracilis*: (11) forebody of sexually mature specimen, (12) ventral and dorsal bundle of chaetae in situ; (13, 14) *Lamprodrilus melanotus*: (13) forebody of sexually mature specimen, (14) chaeta; (15, 16) *Lamprodrilus pallidus*: (15) anterior end, (16) chaeta; (17–20): *Lamprodrilus inflatus*: (17) anterior end, (18) anterior chaeta, (19) chaeta from midbody, (20) posterior chaeta; (21) *Teleuscolex korotneffi*, anterior end; (22) *Teleuscolex glaber*, anterior end; (23–25): *Styloscolex burowi*: (23) anterior end, (24) chaeta, (25) penis sheath; (26–28): *Styloscolex asymmetricus*: (26) forebody of sexually mature specimen, (27) chaeta, (28) penis sheath; (29, 30) *Rhynchelmis brachycephala*: (29) anterior end with tentacle, (30) anterior end without tentacle; (31, 32): *Pseudorhynchelmis anomala*: (31) anterior end, (32) chaetae; (33–35): *Pseudorhynchelmis spermatochaeta*: (33) anterior end, (34) ordinary chaeta, (35) spermathecal chaeta.

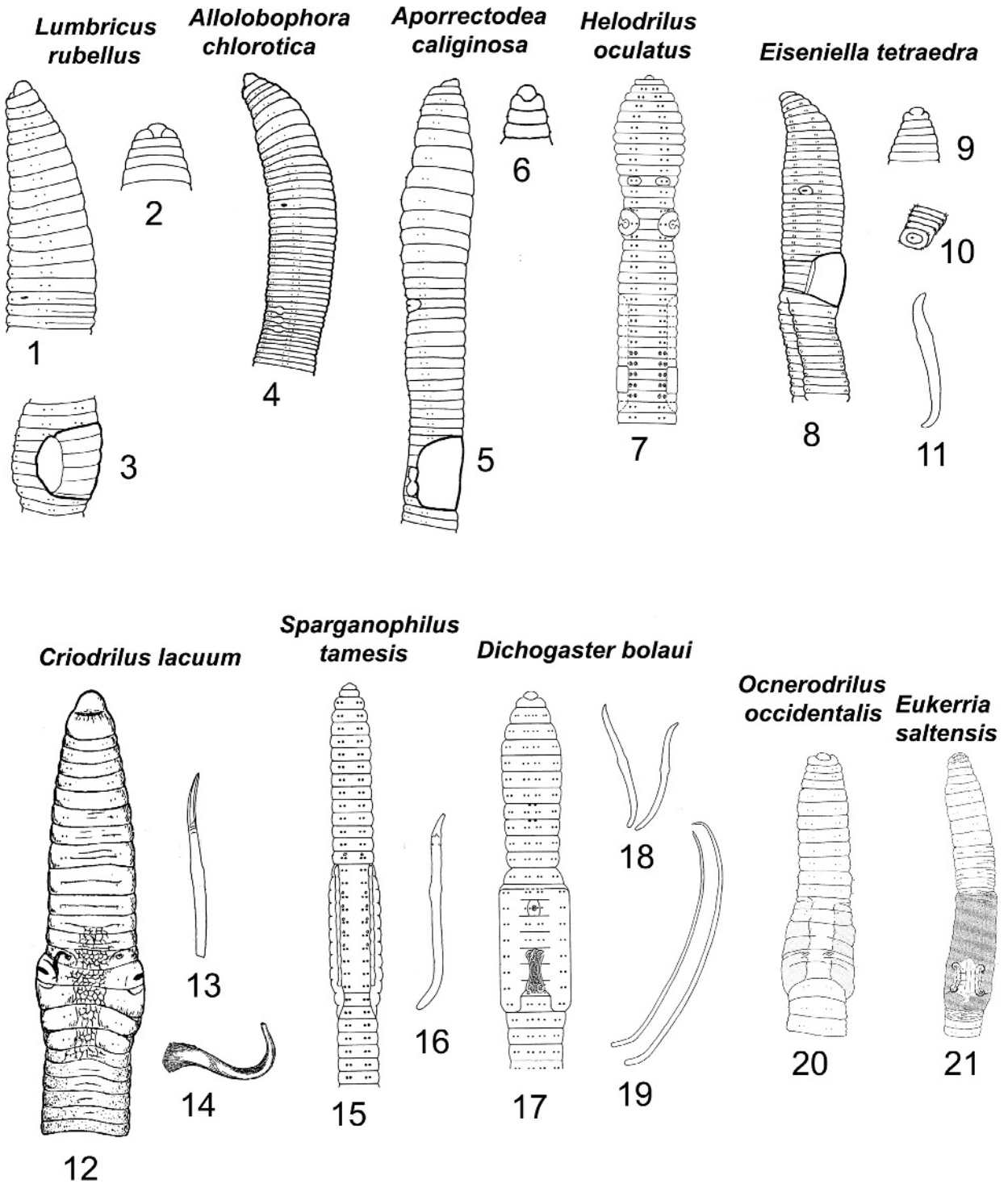


FIGURE 12.28 Lumbricidae and other Crassiclitellata: (1–3): *Lumbricus rubellus*: (1) anterior end in side view, (2) anterior end in dorsal view, (3) genital region with clitellum and *tuberculum pubertatis*; (4) *Allolobophora chlorotica*, maturing specimen with *tubercula pubertatis*; (5, 6): *Aporrectodea caliginosa*: (5) forebody of sexually mature specimen with clitellum and *tubercula pubertatis*, (6) anterior end in dorsal view; (7) *Helodrilus oculatus*, forebody of sexually mature specimen in ventral view with glandular pads and *tubercula pubertatis* (8–11): *Eiseniella tetraedra*: (8) forebody of sexually mature specimen with clitellum and *tubercula pubertatis*, (9) anterior end in dorsal view, (10) posterior end, (11) chaeta; (12–14): *Criodrilus lacuum*: (12) forebody of sexually mature specimen in ventral view with glandular pads, beginning of clitellum and a spermatophore, (13) genital chaeta, (14) spermatophore; (15, 16) *Sparganophilus tamesis*: (15) forebody of sexually mature specimen in ventral view with clitellum and *tubercula pubertatis*, (16) chaeta; (17–19): *Dichogaster bolaui*: (17) forebody of sexually mature specimen in ventral view with clitellum; (18) bundle of ordinary chaetae, (19) bundle of penial chaetae; (20) *Ocnerodrilus occidentalis*, forebody of sexually mature specimen in ventral view with clitellum; (21) *Eukerria saltensis*, forebody of sexually mature specimen in ventral view with clitellum.

6(4) Chaetae very long, in midbody with upper tooth modified as row of small denticles arranged transversely to chaetal axis; secondary annulation from VI; L ≤ 10 mm ..... *Stylodrilus subitus* Semernoy, 2004 [Lake Baikal]

6′ Chaetae with upper tooth modified as small denticles arranged along the chaetal axis; secondary annulation from VIII; L = 5−8 mm (Fig. 12.27(5−7)) ..... *Stylodrilus insperatus* Semernoy, 2004 [Lake Baikal]

7(1) Penes conical, in short penial sacs; secondary annulation from VII 8

7′ Penes different 9

8(7) Penial sacs muscular; atria pyriform; L ≥ 3.5 mm ..... *Stylodrilus contractus* Semernoy, 2004 [Lake Baikal]

8′ Penial sacs thin-walled; atria short tubular; L ≥ 10 mm ..... *Stylodrilus elongatus* Semernoy, 2004 [Lake Baikal]

9(7) Penes short, conical, without sac 10

9′ Penes formed by thin distal portion of atrial duct hidden in very long, thick-walled muscular penial sac, suspended on thin muscles connecting with sac wall; secondary annulation from IX; L ≥ 20 mm (Fig. 12.27(8−10)) ..... *Stylodrilus mirandus* (Hrabě, 1982) [Lake Baikal]

10(9) No penial bulbs; small conical penes persistently protruded; anteriormost chaetae not particularly long 11

10′ Thin-walled penes protruding from penial bulbs; secondary annulation from VII; chaetae in anteriormost segments longer than rest; L ≥ 10 mm (Fig. 12.27(11, 12)) ..... *Stylodrilus gracilis* Semernoy, 2004 [Lake Baikal]

11(10) Atria pyriform; secondary annulation from IX; L = 8 mm ..... *Stylodrilus minutus* Hrabě, 1970 [Lake Baikal]

11′ Atria long tubular, reaching posteriorly to XIV–XV; secondary annulation from V; L ≥ 3 mm ..... *Stylodrilus aclotudi* Kaygorodova & Martin, 2008 [Lake Baikal]

Oligochaeta: Lumbriculida: Lumbriculidae: *Lamprodrilus*: Species (Lake Baikal)

1 Chaetae present beginning from II in all ventral segments at least 2

1′ Chaetae lacking either completely or only in some body regions; general appearance as a nematode; atria elongate, ducts short, surrounded by thick gland mass; conical penes in small penial sacs; L = 5−10 mm (Fig. 12.26(23)) ..... *Lamprodrilus achaetus* Izosimov, 1962 [Lake Baikal; Karelia; Finland]

2(1) Spermathecal pores like male pores, on ventral chaetae line 3

2′ Spermathecal pores lateral in XIII; sacculate ampullae abruptly separated from narrow ducts; atria short, tubular, penes in tiny penial sacs sitting on high external papillae; chaetae sigmoid with noticeably distal nodulus; L = 12−15 mm ..... *Lamprodrilus secernus* Semernoy, 2004 [Lake Baikal]

3(2) Testes and atria two pairs 4

3′ Testes and atria 3−4 pairs, in VIII–XI or IX–XI; atria short, tubular, conical penes in sacs with small penial bulbs; copulatory glands large, in segments following those with male pores; every gland opening on a muscular, phalliform papilla sitting in a respective sac; spermathecae number variable, 1−5 pairs, consisting of a small suboval ampulla and thick muscular duct ending with a muscular papilla; midbody segments with one dorsolateral blood vessel pair; L = 40−115 mm ..... *Lamprodrilus satyriscus* Michaelsen, 1901 [Lake Baikal and Enisej River in Siberia]

4(3) Spermathecae a single pair 5

4′ Spermathecae two pairs, in XIII and XIV or in XII and XIII; atria and male pores either in X and XI or in IX and X; two pairs of dorsolateral blind, chloragogen-covered blood vessels in midbody segments beginning from XXXV; L = 30 mm ..... *Lamprodrilus novikovae* Hrabě, 1982 [Lake Baikal]

5(4) Ventral chaetae very long and thin; dorsal chaetae shorter or lacking; relatively thick worms living at maximum depths 6

5′ Ventral and dorsal chaetae present, similar 7

6(5) No dorsal chaetae, ventral chaetae almost filiform; prostomium with a small tentacle; atria tubular, covered with prostate cells, ending with small conical penis in penial sac; spermathecae with suboval ampulla and clearly separated thick-walled duct; L ≤ 70 mm, diameter 8 mm ..... *Lamprodrilus bythius* Michaelsen, 1905 [Lake Baikal]

6′ Dorsal chaetae present, shorter and thicker than ventral; no tentacle; atria tubular, without prostate cells; spermathecae with suboval ampulla and long duct; L ≤ 30 mm, diameter 5 mm (Fig. 12.27(17–20)) ..... *Lamprodrilus inflatus* Michaelsen, 1905 [Lake Baikal]

7(5) No dorsal dark spot in I–III 8

7′ A single, median dark spot in I–III, formed by dark chloragogen tissue covering dorsal blood vessel to anterior end; longitudinal muscle layer of body wall very thick; blind dorsal blood vessels beginning from XVII, two pairs per segment; atria elongate, spermathecae pyriform; L = 28–32 mm ..... *Lamprodrilus stigmatias* Michaelsen, 1901 [Lake Baikal]

8(7) No transverse glandular pit in XI–XII; a longitudinal glandular furrow present or lacking in X–XIII 9

8′ A small medial, transverse glandular pit on the ventral side of XII or both XI and XII; body wall thin; atria very long, ending with large hemispherical glandular bulbs; spermathecae with large pyriform ampulla and very thin, short duct; L = ∼22 mm ..... *Lamprodrilus ammophagus* Michaelsen, 1905 [Lake Baikal]

9(8) Intersegmental furrows inconspicuous or lacking 10

9′ Intersegmental furrows distinct 13

10(9) No blind transversal blood vessels 11

10′ Blind transversal blood vessels present; atria tubular, ending with penial bulbs without distinct penes; cuticle thick, iridescent; body externally nematode-like; L = 30–42 mm ..... *Lamprodrilus wagneri* Michaelsen, 1901 [Lake Baikal, Angara and Enisej River]

11(10) Ventral glandular furrow or copulatory glands in X–XIII 12

11′ No additional genital glands; atria short, tubular, their short ducts surrounded by thick mass of glands; conical penes in small penial sacs; spermathecal ampullae long sacculate, passing through several segments, abruptly separated from narrow ducts; L = 9–20 mm ..... *Lamprodrilus pygmaeus pygmaeus* Michaelsen, 1901 [Lake Baikal; Eastern Siberia; Karelia (introduced)]

12(11) Ventral glandular furrow present under nerve chain in X–XIII; atria tubular, short ducts surrounded by thick glandular mass; conical penes in small penial sacs; spermathecal ampullae long sacculate, passing through several segments, abruptly separated from the narrow ducts; L = 9–20 mm ..... *Lamprodrilus pygmaeus sulcatus* Izosimov, 1962 [Lake Baikal]

12′ Copulatory gland present after one of male pores and before spermathecal pore, both on one side; atria very long, tubular, short ducts surrounded by thick glandular mass; conical penes in small penial sacs; spermathecal ampullae long sacculate, passing through several segments, gradually transitioning into short ducts; L = ∼20 mm ..... *Lamprodrilus glandulosus* Michaelsen, 1901 [Lake Baikal]

13(9) Body wall coelothelium pigmented 14

13′ Body wall coelothelium not pigmented 15

14(13) Pigment as black spots, particularly in forebody; atria prolonged, with thin duct penetrating glandular mass and opening on small conical penis surrounded with circular fold; spermathecae consisting of suboval ampulla and distinctly separate, rather long duct L = 16–30 mm ..... *Lamprodrilus nigrescens* Michaelsen, 1903 [Lake Baikal]

14′ Pigment uniformly distributed, worm gray; ectal epithelium very thick; chaetae large and thick, almost straight but with curved distal end; atria elongate, thick-walled, penes wide conic, without bulbs but with large glands; spermathecae large, with oval ampulla and distinctly separated narrow duct; abundant cylindrical blind blood vessels beginning from XIX; L = 24–32 m (Fig. 12.27(13, 14)) ..... *Lamprodrilus melanotus* Izosimov, 1962 [Lake Baikal]

15(13) Blind transverse blood vessels in forebody small or lacking 16

15′ Blind transverse blood vessels very large, filling forebody cavity to prostomium; chaetae long, thin, distal end strongly curved; atria tubular, conical penes in penial sacs; L = ∼35 mm ..... *Lamprodrilus dybowskii* Michaelsen, 1905 [Lake Baikal]

16(15) Penial bulbs small or lacking 17

16′ Penial bulbs beside penial sacs very large, with phalliform papillae in sacs; penes short conical; atria long, tubular; spermathecae with short sacculate ampulla, gradually transitioning into short, thick-walled duct; L = 30 mm ..... *Lamprodrilus bulbosus* Izosimov, 1962 [Lake Baikal]

17(16) Chaetae distinctly sigmoid 18

17′ Chaetae thin and almost straight; only distal end slightly hooked; atria elongate, penial bulbs weakly developed, transitioning into thin conical penis with thick cuticle proximally, thin distally, in penial sac; spermathecae with sacculate ampulla gradually transitioning into duct; L = 20–30 mm (Fig. 12.27(15, 16)) ..... *Lamprodrilus pallidus* Michaelsen, 1905 [Lake Baikal]

18(17) Secondary annulation lacking 19

18′ Secondary annulation present; cuticle thin, body wall epithelium and muscular layers thick; blind dorsolateral blood vessels beginning in XX, at first simple, posteriorly branching; similar branching blind vessels from intestinal blood plexus; atria tubular, male pores without penial bulbs; spermathecae simple pyriform; L = 58 mm ..... *Lamprodrilus polytoreutus* Michaelsen, 1901 [Lake Baikal]

19(18) Blind dorsolateral blood vessels beginning from XIX, six per segment, branching; body wall epithelium very thick, muscular layers thin; atria elongate, male pores without penial bulbs or sacs; spermathecae with large oval ampullae and distinctly separated short ducts; L = 55 mm ..... *Lamprodrilus semenkevichi* Michaelsen, 1901 [Lake Baikal]

19′ Blind transverse blood vessels lacking; atria tubular, short ducts surrounded by thick glandular mass; conical penes in small penial sacs; spermathecal ampullae long, sacculate, reaching XIV, abruptly separate from narrow ducts; L = 20–40 mm (Fig. 12.26(17, 18)) ..... *Lamprodrilus isoporus* Michaelsen, 1901 [Lake Baikal; Lake Taimyr in Siberia; northern Europe]

Oligochaeta: Lumbriculida: Lumbriculidae: *Teleuscolex*: Species (Lake Baikal)

1 Copulatory glands lacking 2

1′ Copulatory glands present after the male pores in X 3

2(1) Forebody transversely striped with pigmented lines on each segment; intersegmental furrows distinct; prostomium sharp conical; cuticle thick; atria pyriform or tubular, conical penes in penial sacs; spermathecal ampulla suboval, duct thick walled; L ≤ 115 mm, diameter 4.5 mm (Fig. 12.27(21)) ..... *Teleuscolex korotneffi* Michaelsen, 1901 [Lake Baikal]

2′ No transverse stripes; intersegmental furrows weak; atria cylindrical, large glandular bulbs present, small conical penes in deep penial sacs; spermathecal ampulla pyriform, duct very short; L = 75 mm, diameter 3.8 mm ..... *Teleuscolex baicalensis* (Grube, 1873) [Lake Baikal]

3(1) Intersegmental furrows distinct; atria long, tubular, male pores on small papillae, copulatory glands large; spermathecal ampulla sacculiform, duct short; L ≥ 35 mm, diameter 1.5 mm ..... *Teleuscolex grubei* Michaelsen, 1901 [Lake Baikal]

3′ Intersegmental furrows lacking, body as a nematode; prostomium small, conical; atria long tubular, male pores with or without small penes; large copulatory glands opening on papillae; L = ?, diameter 1.7 mm (Fig. 12.27(22)) ..... *Teleuscolex glaber* Hrabě, 1982 [Lake Baikal]

Oligochaeta: Lumbriculida: Lumbriculidae: *Styloscolex*: Species (Lake Baikal)

1 Spermathecae one single pair in VI–VIII, before atrial segment 2

1′ Spermathecae two pairs in VII and IX; atria long tubular, with penis in VIII, proximal end reaching X; L = 25 mm, diameter 0.72 mm ..... *Styloscolex tetrathecus* Burow, 1931 [Lake Baikal; northeastern Russia; China; Japan]

2(1) Large worms, 3–4 mm diameter, with very thick body wall 3

2′ Smaller worms, less than 1.5 mm diameter 4

3(2) Spermathecae in VI, testes and atria in VII, ovaries in IX; atria sacculate-cylindrical, covered with thick layer of prostate cells; penes thin, styliform; spermathecal ampullae with small distal diverticulum, ducts dilated medially, pores very large and glandular; L = 50 mm, diameter 4 mm ..... *Styloscolex swarczewskii* Burow, 1931 [Lake Baikal]

3′ Spermathecae in VII, testes and atria in VIII, ovaries in X; functioning female funnels in X, two pairs of rudimentary female funnels in XI and XII; atria in VIII, sacculate, covered with layer of prostate cells; L = 50 mm, diameter 3 mm ..... *Styloscolex kolmakovi* Burow, 1931 [Lake Baikal]

4(2) Atria tubular; penes retractable 5

4′ Atria short, cylindrical, covered with prostate cells; penes styliform, in thin tubular sheaths, presumably not retractable; spermathecal duct short and muscular; external segmentation inconspicuous; dorsal chaetae strongly curved distally; L = 4 mm, diameter 0.75 mm (Fig. 12.27(23–25)) ..... *Styloscolex burowi* Semernoy, 2004 [Lake Baikal]

5(4) Penes short, conical 6

5′ Penes cylindrical 7

6(5) Location of genital apparatus variable, with testes and atria in segments VI, VII, or VIII, spermathecae one segment forward, and ovaries two segments posterior; rudiments of these organs may occur in neighboring segments; atria tubular, with groups of prostate cells; spermathecae with ampulla pyriform, short duct thick-walled, confined to one segment; L = 25−30 mm, diameter 1.4 mm ..... *Styloscolex solzanicus* Hrabě, 1982
[Lake Baikal]

6′ Spermathecae always with pores in VII and ampullae reaching the neighboring segments, one ampulla directed anteriorly, one posteriorly; male pores always in VIII, atria tubular, covered with prostate cells, reaching XI; L = 18−20 mm, diameter 0.6 mm (Fig. 12.27(26−28)) ..... *Styloscolex asymmetricus* Izosimov, 1962
[Lake Baikal]

7(5) Atrial ampulla with continuous layer prostate cells; atria reaching X–XI; penes long and thin; chaetae relatively long, thin, straight; spermathecae may contain sperm and long rods of amorphous matter; L = 20−25 mm, diameter 0.75−0.90 mm ..... *Styloscolex chorioidalis* Izosimov, 1962
[Lake Baikal]

7′ Atrial ampulla with prostate cells in groups; tubular atria proximal portion without prostate cover; penes long, thin, with small distal knob; body wall thin; L = 20−40 mm, diameter 0.56−1 mm ..... *Styloscolex baicalensis* Michaelsen, 1901
[Lake Baikal]

Oligochaeta: Lumbriculida: Lumbriculidae: *Pseudorhynchelmis*: Species (Lake Baikal)

Follows Martin & Kaygorodova (2008).

1 Modified genital (spermathecal in VIII or penial in X) chaetae present 2

1′ Modified genital chaetae absent 6

2(1) Penial chaetae in X 3

2′ Penial chaetae absent; spermathecal chaetae in VIII, with medial nodulus and much larger than the rest; atria sacciform, with muscular wall and sparse prostate cover; penes in small penial sacs; spermathecae ampulla bipartite, duct tubular, separated from ampulla by muscular sphincter, distally dilated; L = ∼20 mm (Fig. 12.27(33−35)) ..... *Pseudorhynchelmis spermatochaeta* (Semernoy, 1982)
[Lake Baikal]

3(2) Spermathecal papillae present, as thickening of body epithelium surrounding or behind spermathecal pores; atria cylindrical, to XI or XII; massive copulatory glands surrounding penial chaetae; penial chaetae with nodulus on lower ental third, ectal tips grooved 4

3′ Spermathecal papilla absent; atria tubular, confined to X; copulatory glands surrounding penial chaetae massive or reduced; penial chaetae nodulus slightly proximal to median position, ectal tip ungrooved 5

4(3) Spermathecal ducts opening through massive bulbs; spermathecal papillae behind spermathecal pores, extending toward 8/9; male pores separated from copulatory gland pores by a distance subequal to penial chaetae length; atria extending to XII; L = 24 mm ..... *Pseudorhynchelmis alyonae* (Martin, Ferraguti & Kaygorodova, 1998)
[Lake Baikal]

4′ Spermathecal ducts opening through small vestibulae; spermathecal papillae surrounding spermathecal pores; copulatory gland pores opening close to male pores; atria extending to XI; L = 28 mm ..... *Pseudorhynchelmis olchonensis* (Burow & Koshow, 1932)
[Lake Baikal]

5(3) Prostomium conical; penial chaetae surrounded entally with large copulatory glands and ectally with sucker-shaped genital papillae; atria cylindrical, with large lumen and relatively thin muscular wall; spermathecae ampulla suboval, duct long, tubular, without vestibulum; L ≥ 10 mm ..... *Pseudorhynchelmis semernoyi* Martin & Kaygorodova, 2008
[Lake Baikal]

5′ Prostomium suboval; no genital papillae in X; penial chaetae surrounded entally with small, reduced copulatory glands; atria elongate sacciform, with large lumen and thick muscular wall; spermathecae ampulla voluminous, divided into two pouches (in VIII and IX), duct tubular, ending with a dilated vestibulum lined with thicker cuticle; L = 12.5−16 mm ..... *Pseudorhynchelmis parva* (Michaelsen, 1905)
[Lake Baikal]

6(1) Atrial ampullae elongate, reaching XI 7

6′ Atrial ampullae pyriform, duct short, confined to X; spermathecae with sacculate ampulla and distinctly separate tubular duct; L = 20 mm ..... *Pseudorhynchelmis minimaris* (Semernoy, 2004)
[Lake Baikal]

7(6) Vasa deferentia uniform along their length; penes small, in penial sacs; spermathecal ampullae large and bipartite, occupying VIII and IX; ducts long, tubular; L = 15 mm ..... *Pseudorhynchelmis shamanensis* Martin & Kaygorodova, 1998
[Lake Baikal]

7′ Vasa deferentia dilated medially; spermathecae with sacculate ampulla and twice shorter narrow duct; L = 35 mm; validity of this species is doubtful (Fig. 12.27(31, 32)) ..... *Pseudorhynchelmis anomala* (Semernoy, 2004)
[Lake Baikal]

Oligochaeta: Haplotaxida: Haplotaxidae: Genera

1 Chaetae paired; prostomium not longer than wide; no muscular gizzard; pharyngeal glands present 2

1′ Chaetae one per bundle, simple-pointed, can be sickle-shaped; dorsal chaetae much smaller, can be partially or completely lacking. Prostomium prolonged, forming together with an extension of the mouth segment a short proboscis. No pharyngeal glands; a muscular gizzard present ..... ***Haplotaxis*** **[p. 478]**

2(1) Bifid chaetae present 3

2′ All chaetae single-pointed. The dorsal chaetae can be slightly smaller than ventral 4

3(2) Chaetae sigmoid and sharp, each bundle with a nodulate bifid chaeta with much shorter upper tooth, and another with single sharp tip, without nodulus; body wall rich in transverse rows of unicellular glands, three in every segment, plus multicellular glands associated with dorsal chaetal bundles; no chloragogen tissue at intestine; pharyngeal glands at 5/6–7/8; spermathecae four pairs, with pores in 5/6–8/9; L = 85−137 mm (Fig. 12.24(18, 19)) ..... *Heterochaetella glandularis* Yamaguchi, 1953 [Japan]

3′ Most chaetae bifid with shorter upper tooth, some with 1−2 intermediate denticles; dorsal chaetae slightly longer and thinner than ventral; pharyngeal glands in IV–VI; intestine dilated in VI–VIII; very large, tubular copulatory glands four pairs, vith ventral pores in X–XIII; spermathecae small, either in IV or in VIII; L = 30 mm; springs (Fig. 12.24(5−8)) ..... *Adenodrilus denticulatus* Čekanovskaja, 1959 [Uzbekistan]

4(2) Chaetae obtusely simple-pointed, with nodulus, unornamented, in forebody two and of uniform size, in mid- and hindbody single, dorsal smaller than ventral; cuticle thickened in forebody; pharyngeal glands in III–VI; copulatory glands present inside XI at the body wall; one pair of ovaria in XII; spermathecae 1−2 pairs in VII–VIII or VIII–IX; L = 30−35 mm ..... *Pelodrilus ignatovi* Michaelsen, 1903 [Russia: Lake Teleckoe in Altai Mountains]

4′ Larger worms, at least 2 mm diameter; "dorsal" bundles located very low, actually ventrolateral; chaetae longest in midbody; spermathecae three pairs with pores in 5/6–7/8 on "dorsal" chaetae line; two pairs of ovaria in XII and XIII; clitellum and genital pores externally inconspicuous ..... ***Delaya*** **[p. 478]**

Oligochaeta: Haplotaxida: Haplotaxidae: *Haplotaxis*: Species

1 Dorsal chaetae present at least in younger individuals, can be lacking in the anteriormost segments; no giant chaetae in midbody; all chaetae with nodulus; muscular stomach (gizzard) well developed; two pairs of ovaries, in XII and XIII 2

1′ No dorsal chaetae; ventral chaetae single per bundle (only two per segment), slightly sigmoid without nodulus, of varying size: ≤500 μm long and 45 μm thick in XX, gradually diminishing to 200 μm long and 10 μm thick both in anterior and posterior directions; muscular stomach (gizzard) vestigial; prostomium suboval conical, longer than wide; two pairs of testes in X and XI, one pair of ovaries in XII; two pairs of spermathecal pores lateral in 7/8 and 8/9; L = 50−72 mm; groundwater (Fig. 12.24(9−17)) ..... *Haplotaxis gastrochaetus* Yamaguchi, 1953 [Japan]

2(1) Ventral chaetae in XII–XIV with large glands but not modified 3

2′ Ventral chaetae in XII–XI with large glands and modified as genital chaetae, thinner and straighter than rest, only distal end strongly curved; ventral chaetae largest and distally most arcuate in midbody (about XX); clitellum in X–XIX, weakly developed; spermathecae three pairs, with lateral pores in 6/7–8/9; L ≤ 73 mm ..... *Haplotaxis dubius* (Hrabě, 1931) [Albania/Macedonia: Lake Ohrid]

3(2) Copulatory glands at nerve chain in ½XI–XIV; clitellum in X–XIII; spermathecae three pairs, with lateral pores in 6/7–8/9; L = ∼300 mm; stenothermic, in groundwater and surface waterbodies (Fig. 12.24(1−4)) ..... *Haplotaxis gordioides* (Hartmann, 1821) [Holarctic]

3′ Copulatory glands at nerve chain in IV–XVIII; clitellum in XI–XVI (XVIII, XXV, XXXIII?), yellowish red; dark lateral lines clearly visible; spermathecae four pairs, with pores in 5/6–8/9; L = 50−120 mm ..... *Haplotaxis ascaridoides* Michaelsen, 1905 [Russia: Lake Baikal and Lake Teleckoe]

Oligochaeta: Haplotaxida: Haplotaxidae: *Delaya*: Species

1 Chaetae length variable in same bundle, in midbody tips wearing a thin dorsal keel (upper tooth relict?) which may be worn off; ventral chaetae in IX–XII with large glands; sperm sacs in IX–XII 2

1′ Chaetae without keel, ornamented with tiny hollows in distal curved portion 3

2(1) Chaetae with keel, unornamented; clitellum in X–XVI (XVII, XVIII); L = 100−300 mm, maximum diameter 2.8 mm; caves ..... *Delaya leruthi* (Hrabě, 1958) [France]

2′ Chaetae with keel and distal curved portion ornamented; clitellum in XI–XVI; L = ~100 mm, maximum diameter 2–3 mm; caves .... *Delaya navarrensis* (Delay, 1973) [Spain]

3(1) Glands at more than three pairs of ventral chaetae 4

3′ Ventral chaetal glands in IX–XI; clitellum in X–XVI (XVII, XVIII); L = ~100 mm, maximum diameter 2 mm; caves .... *Delaya cantabronensis* (Delay, 1973) [Spain]

4(3) Ventral chaetal glands in VIII–XIII, largest in XIII; pharyngeal glands only immediately at pharynx; clitellum in XI–XVI; L = ~100 mm, diameter 3 mm; caves .... *Delaya corbarensis* (Delay, 1972) [France]

4′ Ventral chaetal glands mostly in VII–XII; pharyngeal glands small and irregular, up to VIII but not attached to dissepiments; clitellum in XI–XVII; L = 100–170 mm, maximum diameter 5 mm; caves .... *Delaya bureschi* (Michaelsen, 1925) [Balkan Peninsula]

Oligochaeta: Families (Caspian Sea)

1 Reproduction only sexual, male pores and beginning of clitellum in X, XI or XII; dorsal chaetae present beginning from II or III 2

1′ Asexual reproduction by paratomy (with forming of budding zones) prevailing; when sexually mature, male pore and beginning of clitellum in V or VI; dorsal chaetae beginning in III, V, or VI (or completely lacking), hair chaetae present or lacking; small, transparent worms, many able to swim .... **Naididae [p. 479]**

2(1) Male pores and beginning of clitellum in X or XII; no hair chaetae; shorter chaetae either simple or with reduced upper tooth 3

2′ Male pores and beginning of clitellum in XI (may be shifted anteriorly or posteriorly 1–2 segments); dorsal hair chaetae present or absent; shorter, sigmoid chaetae bifid, number in bundle variable .... **Tubificidae [p. 480]**

3(2) Male pores and beginning of clitellum in XII; chaetae without nodulus, straight and simple-pointed, either paired or variable number .... **Enchytraeidae**, one genus: ***Marionina*** **[p. 481]**

3′ Male pores and beginning of clitellum in X; chaetae with nodulus, sigmoid, simple pointed or with reduced upper tooth, always strongly paired .... **Lumbriculidae [p. 482]**

Oligochaeta: Naididae: Genera (Caspian Sea)

1 Dorsal chaetae and prostomium present 2

1′ Dorsal chaetae lacking; first five segments fused into cephaliform organ bearing only one pair of ventral chaetal bundles, without prostomium; mouth directed anteriorly; no eyes; L = 2.5–20 mm; freshwater (Fig. 12.5(1–4)) .... *Chaetogaster diaphanus* (Gruithuisen, 1828) [cosmopolitan]

2(1) All chaetae bifid; no eyes 3

2′ Hair and needle chaetae present in dorsal bundles; eyes present; male pores and beginning of clitellum in VI 4

3(2) Dorsal chaetae beginning in III; segment III prolonged; chaetae 3–4 per bundle; male pores and beginning of clitellum in VI; L = 1.5 mm (of the first zooid); brackish water .... *Amphichaeta sannio* Kallstenius, 1892 [western Palaearctic]

3′ Dorsal bundles beginning from V; chaetae 5–7 per bundle in II, 2–4 posteriorly; male pores and beginning of clitellum in V; L = 2–14 mm; brackish water (Fig. 12.5(16–18)) .... *Paranais litoralis* (Müller, 1784) [cosmopolitan]

4(2) Prostomium with a long proboscis and pair of short protruding lobes; hair chaetae 1–3 and needle chaetae 3–4 per bundle, simple-pointed, sharp; ventral chaetae 4–7 per bundle, with much longer upper tooth; L = 5.5–18 mm; freshwater (Fig. 12.7(1–4)) .... *Stylaria lacustris* (Linnaeus, 1767) [Holarctic. Neotropical. Afrotropical]

4′ No proboscis .... ***Nais*** **[p. 479]**

Oligochaeta: Naididae: *Nais*: Species (Caspian Sea)

1 Hair and needle chaetae in dorsal bundles usually 1–2; upper tooth in ventral bifids longer than lower in anterior segments, length becoming subequal posteriorly 2

1′ Dorsal bundles with several hair chaetae and bifid needle chaetae with fine parallel teeth; ventral bifid chaetae upper tooth length twice lower, strongly curved distally, in all segments; L = 2.2−12 mm; fresh- and brackish water (Fig. 12.9(32−35)) ..... *Nais elinguis* Müller, 1774 [cosmopolitan]

2(1) Needle chaetae finely bifid 3

2′ Needle chaetae blunt; L = 4−9 mm; freshwater (Fig. 12.9(1−3)) ..... *Nais simplex* Piguet, 1906 [cosmopolitan]

3(2) Esophagus gradually dilating into midgut; not swimming; L = 1.5−12 mm; freshwater (Fig. 12.9(28−31)) ..... *Nais communis* Piguet, 1906 [cosmopolitan]

3′ Esophagus abruptly dilating into midgut; able to swim; L = 4−10 mm; freshwater (Fig. 12.9(36−39)) ..... *Nais variabilis* Piguet, 1906 [nearly cosmopolitan]

Oligochaeta: Tubificidae: Genera (Caspian Sea)

1 Hair chaetae present in dorsal bundles; no penial sheaths 2

1′ No hair chaetae; penial sheaths present or lacking 5

2(1) Body wall smooth 3

2′ Body wall transversely folded, covered with a secretion layer and attached foreign bodies, thickest in hindbody; dorsal hair and pectinate chaetae as well as ventral bifid chaetae 1−3, pectinate and bifid chaetae teeth subequal length; no modified genital chaetae; L = 7−9 mm; brackish water ..... "*Peloscolex*" *debilis* Finogenova, 1972, incertae sedis

3(2) Spermathecal chaetae thin or lacking; pectinate chaetae in anterior dorsal bundles, with intermediate denticles shorter than main teeth 4

3′ Single thick, spermathecal chaetae in X ..... ***Potamothrix*** [in part; **p. 481**]

4(3) Bifid chaetae present in all ventral bundles, with upper tooth slightly longer in forebody and with subequal teeth, but lower tooth thicker, in hindbody; 1−2 small bifids present also at male pores in XI; L = 10−100 mm; freshwater (Fig. 12.16(26−31)) ..... *Tubifex tubifex* (Müller, 1774)

4′ Ventral chaetae either lacking or modified into genital chaetae in X and XI; bifid chaetae in mid- and hindbody, both dorsal and ventral, thick, with thick and strongly curved lower tooth and small upper tooth ..... ***Psammoryctides*** [in part; **p. 481**]

5(1) Bifid chaetae not enlarging in mid- and hindbody 6

5′ Bifid chaetae in mid- and hindbody, both dorsal and ventral, thick, with thick and strongly curved lower tooth and small upper tooth ..... ***Psammoryctides*** [in part; **p. 481**]

6(5) Modified genital chaetae only in X and of another shape, or lacking 7

6′ Modified genital chaetae, one per bundle, in IX, X, and XI, with upper tooth length ≥ two times lower, which is laterally dilated; ordinary chaetae with shorter upper tooth; no genital chaetae or penial sheaths in XI; L = 25−35 mm; freshwater (Fig. 12.17(24−31)) ..... *Isochaetides michaelseni* (Lastočkin, 1936) [western Palaearctic]

7(6) No modified genital chaetae 8

7′ Single spermathecal chaetae with grooved distal portion, in X ..... ***Potamothrix*** [in part; **p. 481**]

8(7) Chaetae with shorter upper tooth 9

8′ Chaetae with equal teeth, or the upper tooth longer; penis sheaths present 10

9(8) No penis sheaths; posterior chaetae with thick and curved lower tooth ..... ***Psammoryctides*** [in part; **p. 481**]

9′ Chaetae with shorter upper tooth; penis sheaths in XI short, curved truncated cones; spermathecal pore in X single, dorsal; L = 3−4 mm; brackish water ..... *Aktedrilus svetlovi* Finogenova, 1976 [Caspian Sea]

10(8) Chaetae with equally long teeth; penial sheaths cylindrical, with distal fungiform cuff; L = 25−50 mm; freshwater (Fig. 12.19(18−21)) ..... *Limnodrilus profundicola* (Verrill, 1871) [Holarctic]

10′ Anterior chaetae upper tooth slightly longer; penial sheaths funicular, with blind distal end and lateral aperture; L = 5−10 mm; freshwater (Fig. 12.19(34−36)) ..... *Tasserkidrilus acapillatus* (Finogenova, 1972) [Palaearctic]

Oligochaeta: Tubificidae: *Potamothrix*: Species (Caspian Sea)

1 Hair chaetae present in dorsal bundles; no penial sheaths 2

1′ No hair chaetae; penial sheaths present or lacking 3

2(1) Genital segments X−XI ventrally flattened, usually bearing lateral alate appendages; hair and pectinate chaetae present in dorsal bundles; both bifid and pectinate chaetae with subequal teeth; L = 10−21(55) mm; fresh and brackish water ..... *Potamothrix alatus alatus* Finogenova, 1972
[Caspian Sea; Ukraine: Dnepr−Bug Estuary]

2′ No lateral alate appendages in genital segments; hair and bifid chaetae, with slightly shorter upper tooth, present in dorsal bundles; L = 15−21 mm; freshwater (Fig. 12.13(12−14)) ..... *Potamothrix vejdovskyi* (Hrabě, 1941)
[Ponto-Caspian; invasive in Europe and Nearctic]

3(1) Single spermathecal chaetae with grooved distal portion, in X 4

3′ No modified genital chaetae 7

4(3) Single penial chaetae at male pores in XI, with upper tooth several times longer than lower 5

4′ 1−2 ordinary bifid chaetae, with subequal teeth, at male pores in XI; L = 4−7 mm; brackish water ..... *Potamothrix manus* Finogenova, 1976
[Caspian Sea]

5(4) Spermathecal pores ventral 6

5′ Spermathecal pores lateral; ordinary chaetae with subequal teeth; L = 10−15 mm; brackish water ..... *Potamothrix grimmi* (Hrabě, 1950)
[Caspian Sea]

6(5) Ordinary chaetae with subequal teeth; L = 15−40 mm; freshwater (Fig. 12.18(17−20)) ..... *Potamothrix moldaviensis moldaviensis* Vejdovský & Mrázek, 1903
[western Palaearctic. Invasive in Nearctic]

6′ Ordinary chaetae in anterior segments with shorter upper tooth; L = 8−15 mm; brackish water ..... *Potamothrix moldaviensis mitropolskiji* (Hrabě, 1950)
[Caspian Sea]

7(3) Chaetae with longer upper tooth 8

7′ All chaetae with equal teeth or upper tooth slightly shorter; reproductive system often shifted anteriorly or postriorly 1−2 segments; dissepiments 3/4−10/11 thickened; L = ∼20 mm; fresh and brackish water ..... *Potamothrix mrazeki* (Hrabě, 1941)
[Black Sea; Caspian Sea; Danube River]

8(7) Chaetae with upper tooth length ≤two times shorter tooth; dissepiments 3/4−10/11 thickened; L = 20−30 mm; brackish and freshwater ..... *Potamothrix caspicus* (Lastočkin, 1937)
[Black Sea estuaries; Caspian Sea]

8′ Chaetae with upper tooth slightly longer; no thickened dissepiments; L = 7.5 mm; brackish water ..... *Potamothrix cekanovskajae* Finogenova, 1972
[Caspian Sea]

Oligochaeta: Tubificidae: *Psammoryctides*: Species (Caspian Sea)

1 Hair chaetae present 2

1′ No hair chaetae; no ventral chaetae in X and XI; L = 9−13 mm; brackish water ..... *Psammoryctides deserticola lastockini* (Jarošenko, 1948)
[Black Sea estuaries; Caspian Sea]

1 Thin baciliform spermathecal chaetae with grooved distal portion, in X; hair chaetae long, stiff and roughly pilose; L = 25−35 mm; freshwater (Fig. 12.12(38−44)) ..... *Psammoryctides albicola* (Michaelsen, 1901)
[western Palaearctic]

1′ No ventral chaetae in X and XI; hair chaetae shorter than body diameter, pilose; L = 25−30 mm; brackish and freshwater (Fig. 12.16(8−11)) ..... *Psammoryctides deserticola deserticola* (Grimm, 1877)
[Ponto-Caspian Basin, Danube River, Balkan Peninsula, Near East]

Oligochaeta: Enchytraeidae: *Marionina*: Species (Caspian Sea)

1 Chaetae two (3) per bundle, straight but with proximal bend or hook 2

1′ Chaetae more than two (3) per bundle 4

2(1) Both dorsal and ventral chaetae beginning in II; spermathecal ampullae without diverticula 3

2′ Dorsal chaetae lacking in II or II–III; spermathecal ampullae with a ring of sessile diverticula, duct glandular, a crown of glands surrounding ectal end; L = 8−10 mm; marine and brackish littoral, seldom fresh water (Fig. 12.23(34−36)) ..... *Marionina southerni* (Černosvitov, 1937) [Holarctic]

3(2) Chaetae equal length in each pair; spermathecae with prolonged suboval ampulla, its sharp ental end connected with esophagus; distinct ectal duct thick-walled; large gland at spermathecal pore; L = 3 mm; brackish water ..... *Marionina aberrans* Finogenova, 1973 [Caspian Sea]

3′ Chaetae in each pair slightly different in size; spermathecae with small suboval ampulla, longer duct of same width, crown of glands around ectal pore; L = 3−4 mm; brackish water ..... *Marionina mica* Finogenova, 1972 [Ukraine: Black Sea estuaries; Caspian Sea]

4(1) Chaetae in forebody 4−8, in hindbody 3−5 per bundle, straight and sharp, sometimes proximally slightly curved; dorsal blood vessel from IX anteriorly; spermathecae ampulla oval, duct short, narrow, without glands; L = 2.5−3 mm; brackish water ..... *Marionina micula* Finogenova, 1972 [Caspian Sea]

4′ Chaetae in forebody 4−7, in hindbody 2−4 (5) per bundle, straight, obtuse, middle chaetae in each bundle can be shorter; dorsal blood vessel from XI anteriorly; spermathecae ampulla oval or suboval, duct short, narrow with glandular walls; L = 2−4 mm; slightly brackish water (Fig. 12.23(30−33)) ..... *Marionina brevis* Finogenova, 1972 [Ukraine: Black Sea estuaries; Caspian Sea]

Oligochaeta: Lumbriculidae: Genera and Species (Caspian Sea)

1 Chaetae with rudimentary upper tooth; spermathecal pores in IX 2

1′ Chaetae simple-pointed; male pores on small protuberances in X, spermathecal pores in XI and XII; L = ?; brackish water ..... *Trichodrilus pauper* Finogenova, 1973 [Caspian Sea]

2(1) Short conical penes protruding over the body surface in X; L = ?; brackish water ..... *Stylodrilus cernosvitovi* Hrabě, 1950 [Caspian Sea]

2′ No penes; L = 10−15 mm; mainly freshwater (Fig. 12.24(36−38)) ..... *Stylodrilus parvus* (Hrabě & Černosvitov, 1927) [Europe; Turkey; Caspian Sea]

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Subclass Branchiobdellida

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INTRODUCTION

Branchiobdellidans (crayfish worms) are small (adults ranging from 0.8 to 12.0 mm) annelids that live on the exposed surface and in branchial chambers of astacoidean crayfish, although some species have adopted freshwater shrimps. These ectosymbionts can be found in freshwater bodies where their hosts live (see Chapter 16). Branchiobdellidans form a single family order, but to be consistent with the other clitellate taxa in this chapter, branchiobdellidans have been raised in rank to subclass, Branchiobdellidea. In Chapter 20 of Volume I (p. 511), the group was called Branchiobdellida, which is the correct name as the group is considered an order rather than a subclass. The Branchiobdellida currently consists of the Branchiobdellidae with four subfamilies, Branchiobdellinae, Bdellodrilinae, Cambarincolinae and Xironodrilinae (Gelder & Williams, 2015). Using both morphological and molecular data, the Branchiobdellida forms a monophyly within the Clitellata; however, subfamilies are either paraphyletic or polyphyletic (Gelder & Brinkhurst, 1990; Williams et al., 2012). In contrast, a zoogeographical grouping is found with endemic genera being located in either the Palaearctic or Nearctic realms. Palaearctic branchiobdellidans currently total one genus and eight species in the Euro-Mediterranean, and six genera with 37 species in the East Asia regions. Although *Branchiobdella* is common to both regions, species are restricted to their respective endemic region.

LIMITATIONS

With few exceptions, identification of crayfish worms requires microscopic examination of either preserved or live mounted specimens. As many species share similar morphological characters; body length and shape, and jaw structure, additional details of anterior nephridial pore number, male and female reproductive structures, and other morphological features are needed for a definitive identification.

The only branchiobdellidans in the Palaearctic region with limitations on their collection are the Japanese: *Cirrodrilus aomorensis* (Yamaguchi, 1934), *Cirrodrilus cirratus* (Pierantoni, 1905), *Cirrodrilus ezoensis* (Yamaguchi, 1934), *Cirrodrilus homodontus* (Yamaguchi, 1932b), *Cirrodrilus inukaii* (Yamaguchi, 1934), *Cirrodrilus makinoi* (Yamaguchi, 1934), *Cirrodrilus megalodentatus* (Yamaguchi, 1934), *Cirrodrilus nipponicus* (Yamaguchi, 1932c), *Cirrodrilus sapporensis* (Pierantoni, 1906), *Cirrodrilus tsugarensis* Ohtaka & Gelder, 2000, *Cirrodrilus uchidai* (Yamaguchi, 1932a), and these are listed in the Red Data Book by Ohtaka (2014). For collecting restrictions on crustaceans, crayfish, and shrimps, which host branchiobdellidans, see Chapter 24 for further details. In addition, general considerations for collecting have been summarized by Rogers & Thorp (2015, Chapter 3).

TERMINOLOGY AND MORPHOLOGY

Taxonomic and other descriptions of branchiobdellidan morphology use some terms that differ from those used in other annelid groups. Therefore, to avoid confusion all terms used in this branchiobdellidan key are described and external body features are shown in Fig. 12.29. Branchiobdellidans have a distinct head, consisting of a peristomium and three segments, followed by body segments designated 1–11 with Arabic numerals. Oligochaete and leech segments are numbered with Roman numerals;

however, in oligochaetes the peristomium is designated segment I (the prostomium is ignored), while in leeches the prostomium is segment I and the peristomium segment II; branchiobdellidans use the oligochaete system when necessary (Fig. 12.29). Body length and shape are important features, as are ornamentation on the peristomium (lobes and tentacles) and segments [two or three annuli, dorsal ridges supported by supernumerary muscles (Fig. 12.33, sm), dorsal projections, and lateral lobes]. Examples of species with a selection of these features are shown in Figs. 12.30 A–F.

The first identifying character in the dichotomous key is the presence of one or two anterior nephridial pores on the dorsal surface of segment 3 (Figs. 12.31 A, B); this is best determined on live individuals. Internal characters include the paired jaws, their size, shape and number of teeth (Figs. 12.32 A–D). These features are best observed from a dorsal or ventral view when each jaw is slightly displaced. A dental formula consists of the number of teeth on dorsal and ventral jaws, these being expressed as 11/7, 6/5, 7/7, and 7/7 (Figs. 12.32 A–D); however, for greater resolution, Figs. 12.32 C, D are given as 3-1-3/3-1-3. Dentition in many species is variable, e.g., *B. astaci* (Fig. 12.32 A), where some or all of the small teeth can be missing, which results in an apparent dental formula of 1/1. Although the characters just listed may indicate a particular species, the identification remains tentative until the reproductive organ characters located in body segments 5 and 6, have been examined (Fig. 12.33). Relative position of a structure is referred to with reference to the external surface, hence "ectal"—nearest the exterior or "ental"—farthest from the exterior (these terms are equivalent to "proximal" and "distal"). For example, vasa deferentia enter the glandular atrium ectally (Fig. 12.33). When the glandular atrium and prostate gland are both lined with granular cells, the gland is called "undifferentiated," while a prostate gland lined with vacuolar cells is referred to as "differentiated." Some species have a prostatic ental bulb (eb), but its size can vary significantly depending on, presumably, an individual's degree of maturity and preservation conditions. The penis is characterized by its method of extension, being either "protrusible" or "eversible." In the retracted position a protrusible penis is located in the bursa's ental half (Fig. 12.34 A). In the eversible form, the penis consists of a long, folded penial tube in a penial sheath extending from the ental bursa into the muscular atrium (Fig. 12.35 A).

The spermatheca or sperm receptacle (Fig. 12.33) is the only female organ involved in the key and consists of a pore (sp), duct (sd), bulb (sb), and, when present, ental process (ep). In some species it is highly variable in size and shape due to the volume of sperm in the bulb and position at the time of preservation. Generally a spermatheca is located in segment 5, but in *Sinodrilus* it is in segment 6 and absent in *Caridinophilus*.

MATERIAL PREPARATION AND PRESERVATION

Preservation of crustaceans frequently consists of placing them directly into 10% formalin or freezing. Both methods are strongly discouraged for preservation of crayfish worms as formalin is carcinogenic and also hampers many post collection protocols (e.g., protein- or DNA-based analyses), while ice crystals render worm soft tissue characters unrecognizable. Therefore 70% ethanol, isopropanol, or alcohol-formalin-acetic acid (AFA) are the most frequently used preservatives if the crustacean's branchiobdellidans are to be studied; 70% ethanol being the most practical. Preserved crustaceans are immersed in a dish containing 70% ethanol, and then the container debris is checked for worms which are placed in a specimen tube with new 70% ethanol.

Live crustaceans are held immersed in water under a dissection microscope and the external surface and branchial chambers are searched for worms. Branchiobdellidans are removed from the host and container surfaces by stroking the posterior sucker with a mounted needle so the worm transfers to the needle. Then it is transferred to clean water (preferably from the collection site = habitat water) in a small stacking dish and the procedure repeated. Alternatively, a crayfish may be placed in 1:1 mixture of a carbonated beverage (e.g., club soda) and habitat water or a 1%–2% magnesium chloride solution for a short time (1–5 min); concentration and times should be adjusted for each species as necessary for optimal results. Although the host may remain active, many branchiobdellidans will fall off but others will remain attached, particularly in the branchial chamber, so it is necessary to examine the crayfish as described above. At this point branchiobdellidans can be moved to fresh, habitat water to recover, dropped into preservative, or straightened on a microscope slide prior to preserving. An extended time in the anesthetic will kill the worms and allow autolysis to occur as the fluid is not a preservative.

Although branchiobdellidan identification is frequently accomplished with preserved material, several distinguishing characters are most easily determined using "wet mount" preparations of live worms. A live branchiobdellidan is placed in a drop of water on a microscope slide and gently covered with a cover glass. The amount of water on the slide, and thus the mobility of the worm, can be controlled by withdrawing water with a paper tissue or adding more from a pipette. The specimen is examined under a compound microscope to determine external and internal morphological characters are described above. A specimen must be observed from both dorsoventral and lateral aspects to see all identifying characters. Changing the aspect is easily achieved by pushing the cover glass gently so the specimen rolls through a quarter turn.

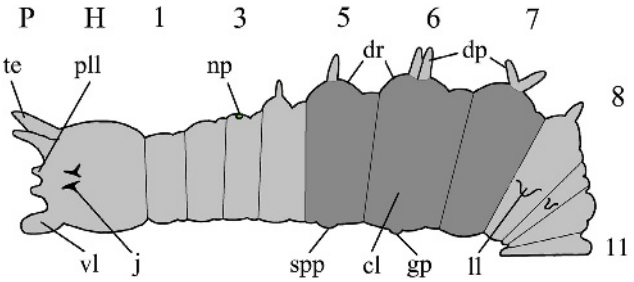


FIGURE 12.29 Lateral view of generalized branchiobdellidan to show most of the external features): 1−11, body segment numbers; *cl*, clitellum; *dp*, dorsal projections; *dr*, dorsal ridge; *gp*, genital pore; *H*, head; *j*, jaw; *ll*, lateral segmental lobes; *np*, anterior nephridial pore; *P*, peristomium; *pll*, peristomial lateral lobe; *spp*, spermatheca pore; *te*, dorsal peristomial lip tentacle; *vl*, ventral peristomial lip (Gelder, 2013).

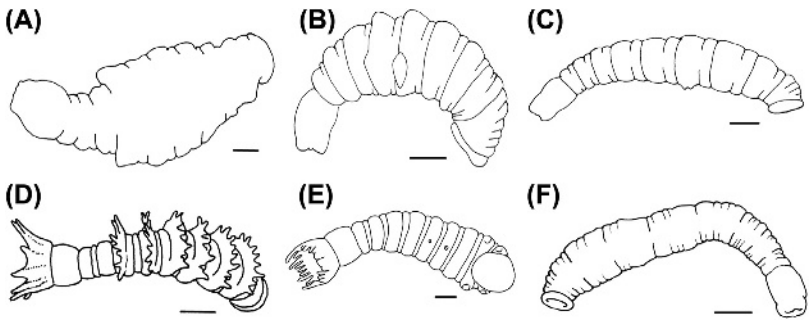


FIGURE 12.30 (A) Ventral view of *Branchiobdella balcanica*, bar = 0.2 mm; (B) Lateral view of *B. domina*, bar = 0.2 mm; (C) Lateral view of *B. hexodonta*, bar = 0.5 mm; (D) Dorsal view of *Cirrodrilus cirratus*, bar = 0.2 mm; (E) Ventral view of *C. suzukii* bar = 0.5 mm; (F) Lateral view of *Holtodrilus truncatus*, bar = 0.2 mm. *(A) From Gelder, 2013; (B) from Timm, 1991; (C) from Pop, 1965; (D) from Yamaguchi, 1934; (E) from Yamaguchi, 1934; (F) from Liang, 1963.*

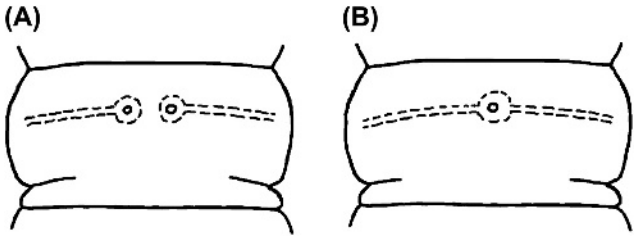


FIGURE 12.31 (A) Anterior nephridial pores on the dorsal surface of segment 3 with underlying collection bulb and ducts (*dashed lines*); (B) Single median nephridial pore. *From Gelder, 2013.*

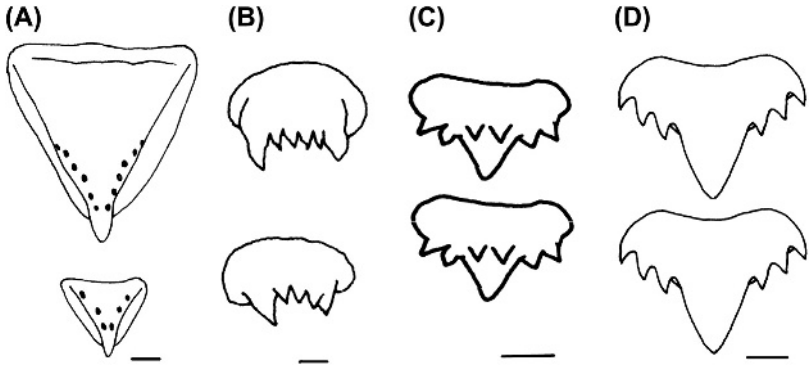


FIGURE 12.32 Branchiobdellidan jaws with dorsal over ventral and teeth pointing posteriorly; (A) *Branchiobdella astaci,* bar = 0.3 mm (Subchev, 1984); (B) *Branchiobdella hexodonta,* bar = 10 µm (Gelder, 2012); (C) *Cirrodrilus kawamurai*, bar = 10 µm (Yamaguchi, 1934); (D) *Holtodrilus truncatus*, bar = 10 µm (Liang, 1963).

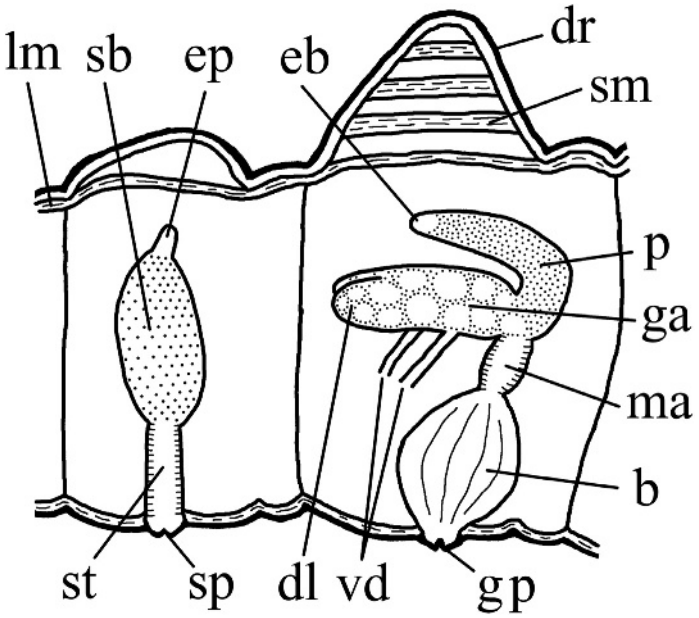


FIGURE 12.33 Lateral view of body segments 5 and 6 showing spermatheca (or female spermatozoa receptacle) and male genitalia: *b*, bursa; *dl*, deferent lobes; *dr*, dorsal ridge; *eb*, ental bulb; *ep*, ental process; *ga*, glandular atrium; *gp*, genital pore; *lm*, longitudinal body muscles; *ma*, muscular atrium; *p*, prostate gland; *sb*, spermatheca bulb; *sm*, supernumerary muscle; *sp*, spermatheca pore; *sd*, spermatheca duct; *vd*, vasa deferentia (Gelder, 2013).

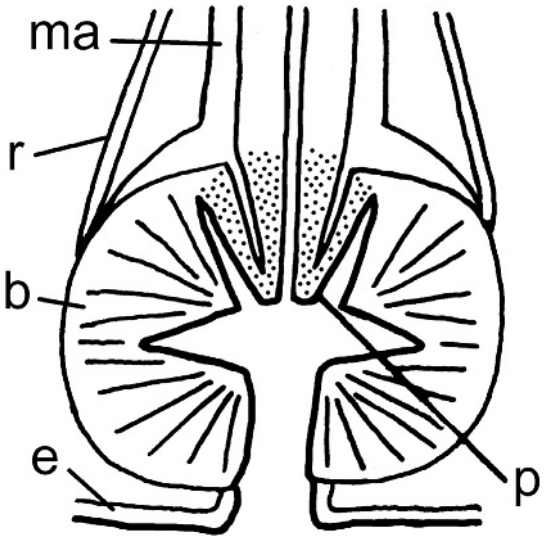


FIGURE 12.34 Schematic longitudinal section through bursa to showing a generalized protrusible penis in retracted position: *b*, bursa; *e*, epidermis; *ma*, muscular atrium; *p*, penis (dotted); *r*, retractor muscle (Gelder, 2013).

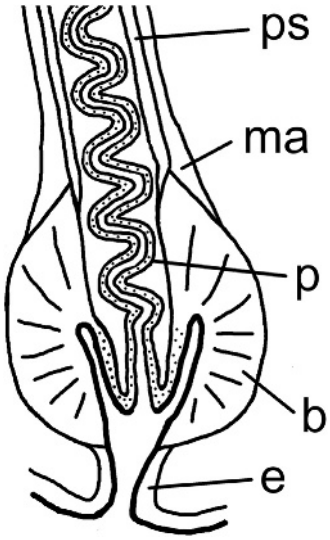


FIGURE 12.35 Schematic longitudinal section through the bursa to show a generalized eversible penis in retracted position: *b*, bursa; *e*, epidermis; *ma*, muscular atrium; *p*, penis (dotted); *ps*, penial sheath (Gelder, 2013).

Although a compound microscope with differential interference contrast (DIC) illumination is best for seeing the morphology, ordinary bright field illumination will enable all features to be adequately determined for identification. Examination of live branchiobdellidans can greatly reduce the time needed for species identification, and leaves a specimen available for subsequent processing (e.g., establishing a culture, for museum curation, histology, electron microscopy, molecular sequencing).

Unstained specimens for species identification are dehydrated in graded water:ethanol solutions, cleared (removal of preservation opacity) in clove oil or oil of wintergreen (methyl salicylate), and mounted in Canada balsam on microscope slides with a cover glass to produce a permanent museum standard preparation. This usually takes 2–3 days and hardening the mountant ranges from 1 to several weeks as it is dependent on the size of the specimen. These clearing agents also add contrast to the specimen's internal organs by having a slightly different refractive index to glass and this replaces the need for staining. As any permanent mount only allows the worm to be seen from one aspect, multiple specimens are needed to see all of the identification characters. Genitalia in large, whole branchiobdellidans (6–10 mm long) may be too big to be seen on slide preparations. Therefore organs are removed by microdissection underwater, then preserved and mounted on a microscope slide by the methods described above. Instruments for this procedure can be made from fragments of a razor blade and insect (very small) pins glued to the end of tooth picks.

Alternative preparation methods for examining branchiobdellidans include clearing mixtures that make semi-permanent microscopical mounts (see microtechnique textbooks or on-line). Specimens in these mountants only last for a few days to several months, and some of the component chemicals (particularly those containing lactic acid) damage branchiobdellidan soft tissues, rendering worms useless for longer-term reference.

KEYS TO BRANCHIOBDELLIDA

Branchiobdellida: Branchiobdellidae: Subfamilies

1	Two anterior nephridial pores (Fig. 12.31 A)	2
1′	One anterior nephridial pore (Fig. 12.31 B)	3
2(1)	Vasa deferentia enter glandular atrium ectally (not terminally, Fig. 12.33)	**Branchiobdellinae [p. 488]**
2′	Vasa deferentia enter glandular atrium entally (terminally)	Xironodrilinae, one species: *Holtodrilus truncatus* (Liang, 1963) [China, Japan, Taiwan]
3(1)	Vasa deferentia enter glandular atrium ectally (not terminally)	**Bdellodrilinae [p. 490]**
3′	Vasa deferentia enter glandular atrium entally (terminally)	**Cambarincolinae [p. 490]**

Branchiobdellinae: Species

1	Testes one pair	2
1′	Testes two pairs in segments 5 and 6	3
2(1)	Testes in segment 5	*Branchiobdella*
2′	Testes in segment 6	*Sinodrilus heterorchis* (Liu & Zhang, 1983) [China, Korean Peninsula]
3	Body shape terete or tubular	*Cirrodrilus*
3′	Body shape tennis racquet shape	*Xironogiton victoriensis* Gelder & Hall, 1990 [Nearctic. Invasive in England, France, Hungary, Italy, Japan, Spain, Sweden]

Branchiobdellinae: *Branchiobdella*: Species

1	Body length greater than 5.0 mm	2
1′	Body length less than 5.0 mm	5
2(1)	Triangular jaws	3
2′	Rectangular jaws	*Branchiobdella hexodonta* Gruber, 1883 [Europe]
3(2)	Jaws, both large	4

3′	Jaws dorsal large and ventral small	*Branchiobdella astaci* Odier, 1823 [Europe]
4(3)	Dental formula 11/11 (5-1-5/5-1-5)	*Branchiobdella orientalis* Yamaguchi, 1934 [China, Korean Peninsula]
4′	Dental formula 5/5 (2-1-2/2-1-2)	*Branchiobdella parasita* (Braun, 1805) [Europe]
5(1)	Body length greater than 1.0 mm	6
5′	Body length less than 1.0 mm	13
6(5)	Dental formula 5/5	7
6′	Dental formula not 5/5	11
7(6)	Jaws triangular	8
7′	Jaws oblong	9
8(7)	Body segment papillae absent	*Branchiobdella cheni* Liu, 1964 [China, southeastern Russia]
8′	Body segment papillae present on segments 3, 8, and 9	*Branchiobdella papillosa* Nesemann & Hutter, 2002 [Austria]
9(7)	Jaws rectangular	10
9′	Jaws square	*Branchiobdella kozarovi* Subchev, 1978 [Bulgaria, Georgia, Iran, Kazakhstan, Poland, Turkey, Ukraine]
10(9)	Spermathecal duct length shorter than bulb	*Branchiobdella pentodonta* Whitman, 1882 [Europe]
10′	Spermathecal duct length longer than bulb	*Branchiobdella italica* Canegallo, 1928 [Croatia, Italy]
11(6)	Body segment lateral extensions present	12
11′	Body segment lateral appendages absent	*Branchiobdella teresae* Subchev, 1986 [Korean Peninsula]
12(11)	Lateral extensions on segment 4	*Branchiobdella balcanica* Moszyński, 1938 [Europe]
12′	Lateral extensions on segments 4 and 5	*Branchiobdella domina* Timm, 1991 [southeastern Russia]
13(5)	Dorsal jaw one tooth	14
13′	Dorsal jaw five teeth	*Branchiobdella minuta* Pierantoni, 1912 [southeastern Russia]
14(13)	Ventral jaw multiple teeth	15
14′	Ventral jaw one tooth	*Branchiobdella monodontus* Liu & Zhang, 1983 [China]
15(14)	Peristomial ventral lip same size as dorsal	*Branchiobdella kobayashii* Yamaguchi, 1934 [China, Korean Peninsula]
15′	Peristomial ventral lip larger than dorsal	*Branchiobdella macroperistomium* Liu & Zhang, 1983 [China, Korean Peninsula]

Branchiobdellinae: *Cirrodrilus*: Species

1	Dorsal body segment appendages present	2
1′	Dorsal body segment appendages absent	3
2(1)	Supra-oral papillae present	*Cirrodrilus cirratus* Pierantoni, 1905 [Japan]
2′	Supra-oral papillae absent	*Cirrodrilus uchidai* (Yamaguchi, 1932) [Japan]
3(2)	Segments 8 and 9 lateral appendages absent	4
3′	Segments 8 and 9 lateral appendages present	13
4(3)	Body length, less than 7.0 mm	5

4′	Body length, greater than 7.0 mm	*Cirrodrilus sapporensis* (Pierantoni, 1906) [Japan]
5(4)	Peristomial dorsal tentacles greater than four	6
5′	Peristomial dorsal tentacles four	*Cirrodrilus kawamurai* (Yamaguchi, 1934) [China, Korean Peninsula]
6(5)	Peristomial dorsal tentacles greater than six	7
6′	Peristomial dorsal tentacles five	*Cirrodrilus peristomialis* (Liu & Chang, 1964) [China]
7(6)	Peristomial dorsal tentacles fewer than six	8
7′	Peristomial dorsal tentacles greater than seven	11
8(7)	Dental formula 9/9 (4-1-4/4-1-4)	9
8′	Dental formula 11/11 (5-1-5/5-1-5)	10
9(8)	Segments 8 and 9 lateral appendages large, conical	*Cirrodrilus pugnax* Timm, 1991 [southeastern Russia]
9′	Segments 8 and 9 lateral appendages small, rounded	*Cirrodrilus quadritentacularis* (Liu, 1984) [China, southeastern Russia]
10(8)	Segments 8 and 9 lateral appendages conical	*Cirrodrilus breviformis* (Liu & Chang, 1964) [China, Korean Peninsula]
10′	Segments 8 and 9 lateral appendages, plate-like	*Cirrodrilus heteroglandularis* (Liu & Chang, 1964) [China]
11(7)	Peristomial dorsal tentacles mixture of long and short	12
11′	Peristomial dorsal tentacles all short	*Cirrodrilus liaoningensis* (Liu & Chang, 1964) [China]
12(11)	Peristomial dorsal tentacles medians two short	*Cirrodrilus fimbriatus* Timm, 1991 [southeastern Russia]
12′	Peristomial dorsal tentacles medians three short	*Cirrodrilus suzukii* (Yamaguchi, 1934) [China, Korean Peninsula, southeastern Russia]
13(3)	Jaw, median large tooth conical	14
13′	Jaw, median large tooth flat-topped	*Cirrodrilus anodontus* (Liu, 1964) [China]
14(13)	Dental formula 7/7 (3-1-3/3-1-3)	15
14′	Dental formula greater than 7/7	16
15(14)	Peristomial dorsal tentacles all short	*Cirrodrilus tsugarensis* Gelder & Ohtaka, 2000 [Japan]
15′	Peristomial dorsal tentacles short and long	*Cirrodrilus aequiannulus* (Liu, 1984) [China]
16(14)	Dental formula 9/9 or greater	17
16′	Dental formula 7/11 (3-1-3/5-1-5)	*Cirrodrilus megalodentatus* (Yamaguchi, 1934) [Japan]
17(16)	Dental formula 9/9	18
17′	Dental formula 10/10 or greater	23
18(17)	Peristomial dorsal tentacles four	19
18′	Peristomial dorsal tentacles greater than four	20
19(18)	Jaws similar size	*Cirrodrilus homodontus* (Yamaguchi, 1932) [Japan]
19′	Jaws dissimilar size (dorsal larger)	*Cirrodrilus ezoensis* (Yamaguchi, 1934) [Japan]
20(18)	Peristomial dorsal tentacles greater than five	21
20′	Peristomial dorsal tentacles five	*Cirrodrilus makinoi* (Yamaguchi, 1934) [Japan: Hokkaido]
21(20)	Peristomial dorsal tentacles greater than seven	22

21′	Peristomial dorsal tentacles seven	*Cirrodrilus aomorensis* (Yamaguchi, 1934) [Japan]
22(21)	Peristomial dorsal tentacles eight	*Cirrodrilus minimus* (Liu, 1964) [China]
22′	Peristomial dorsal tentacles nine	*Cirrodrilus chosen* (Yamaguchi, 1934) [China, Korean Peninsula, southeastern Russia]
23(17)	Dental formula greater than 11/11	24
23′	Dental formula 10/10	*Cirrodrilus iwakiensis* Ohtaka & Gelder, 2015 [Japan]
24(23)	Jaw striations absent	25
24′	Jaw striations present	*Cirrodrilus japonicus* (Pierantoni, 1912) [Japan]
25(24)	Dental formula 11/11 (5-1-5/5-1-5)	*Cirrodrilus inukaii* (Yamaguchi, 1934) [Japan]
25′	Dental formula 15/15 (7-1-7/7-1-7)	*Cirrodrilus nipponicus* (Yamaguchi, 1932) [Japan]

Bdellodrilinae: Species

1	Spermatheca present	*Hidejiodrilus koreanus* Gelder & Brinkhurst, 1990 [Korean Peninsula]
1′	Spermatheca absent	*Caridinophilus unidens* Liang, 1963 [China]

Cambarincolinae: Genera

1	Prostate gland present	2
1′	Prostate gland absent	*Triannulata magna* Goodnight, 1940 [introduced Nearctic species: France]
2	Protrusible penis	***Cambarincola* [p. 490]**
2′	Eversible penis	*Sathodrilus attenuatus* Holt, 1981 [introduced Nearctic species: Japan]

Cambarincolinae: *Cambarincola*: Species

1	Peristomial dorsal lobes slight or absent	2
1′	Peristomial dorsal lobes large	*Cambarincola okadai* Yamaguchi, 1933 [Nearctic.Introduced: England, France]
2(1)	Dental formula 1/4	*Cambarincola gracilis* Robinson, 1954 [Nearctic.Introduced: France]
2′	Dental formula 5/4	*Cambarincola mesochoreus* Hoffman, 1963 [Nearctic. Introduced: Italy]

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Subclass Hirudinida

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INTRODUCTION

Leeches (Hirudinida) are recognizable by having segmented bodies with attachment suckers. Approximately 196 described freshwater, brackish water and terrestrial to semiterrestrial leech species are currently recognized in Eurasia. Leeches are important components of aquatic ecosystems, as predators on invertebrates or ectoparasites on a range of vertebrate hosts. Leeches are used as indicator species for aquatic chemistry and biodiversity, as certain species are connected with specific aquatic conditions and certain types of animals. Leeches inhabit a range of habitats including lakes, ponds, swamps, rivers, streams, and moist soil. Typically leeches are most abundant along shorelines in vegetation and under rocks or other substrates. The full distribution of most leech species is unknown and the paucity of knowledge is due to the lack of regional investigations and the difficulty of identifying some species. The misidentification of species has also led to problems with species concepts and geographic ranges for described species. In addition, recent molecular and morphological studies have revealed numerous errors in leech classification and species concepts, as well as cryptic species and unexpected relationships. It is therefore important that specimen vouchers are deposited in a natural history museum for future analysis. These keys include updated taxonomy and, where possible, use external characteristics to separate taxa.

TERMINOLOGY AND MORPHOLOGY

The following terms are needed to use the keys. **Accessory eyes**: Two pair of variable concentrations of dark pigment situated between two and five annuli behind the single functional pair of eyes (giving the impression of three pairs of eyes) in the cephalic (head) region of *Placobdella hollensis*. Also called accessory ocelli, accessory eyespots or supplementary eyes. **Agnathus**: Complete absence of jaw-like prominences in the pharynx cavity, as in the Erpobdellidae. **Annuli (annulus—sing.)**: External body rings or superficial transverse furrows subdividing each somite. There are essentially three primary annuli, labeled a1, a2, a3. Each can be further subdivided into secondary annuli (b1, b2, to b6) and further subdivided into tertiary annuli (c1, c2, to c12) and rarely subdivided into quaternary annuli (d1, d2 to d24). **Anterior sucker**: The attachment or suction device found at the anterior end of the leech which contains the mouth or mouth pore. Also called the oral sucker or cephalic sucker. **Atrial cornua**: corniform prolongations of the atrium where the sperm ducts (ejaculatory ducts) attach to the atrium. Also called the horn of atrium. **Atrium**: Male reproductive organ consisting of a thin-walled bursa (may be eversible), a thick-walled muscular and glandular medium chamber and a pair of atrial cornua. The atrium opens externally through the male gonopore and, in some species, is modified into an eversible penis. **Buccal cavity**: The mouth chamber which contains muscular ridges that may or may not have jaws attached. Leeches with a proboscis (order Rhynchobdellida) do not possess a buccal cavity. **Caudal ocelli**: Eyespots (ocelli) on the caudal sucker of certain Piscicolids. May be either crescentiform or punctiform. Also called oculiform spots. **Caudal sucker**: The attachment or suction device found at the posterior end of the leech. Also called the posterior sucker or subanal sucker. **Caeca (caecum—sing.)**: Diverticula of the crop (stomach) or intestine, which increases the digestive system surface area. The opposite is the acaecate (without caeca). **Cephalic region**: The head region. **Chromatophore**: A cutaneous pigment cell or group of pigment cells which provide coloration and can be altered in shape and size (under the control of the nervous system). There are three basic chromatophore types: brown cutaneous, cream-colored cutaneous, and green hypodermal. **Clitellum**: A swollen glandular region or saddle of epidermal tissue in the area of the gonopores that secretes material to form cocoons. The area that contains the clitellum is called the clitellar region. **Cocoon**: Chitinous, membranous or spongy structure that is formed by clitellar secretions and contains fertilized eggs. Cocoons are either deposited on a submerged object, in a moist area, or brooded by the adult. **Copulatory depressions**: A ventral glandular area around the gonopores and copulatory pits of *Philobdella* spp. **Copulatory gland pores**: External openings of the copulatory glands, located on the anterior midbody ventral surface and a few annuli posterior to the female gonopore in *Macrobdella* spp. The number and arrangement of copulatory gland pores are a diagnostic character of *Macrobdella* species and exist in a linear or transverse pattern of either 4, 6, 8, or 24. **Copulatory glands**: Glands whose contents exit through the copulatory gland pores, with an uncertain function (may secrete a glandular adhesive—to stick leeches together during copulation). **Copulatory pits**: Thick depressions and prominences of the glandular area around the gonopores of *Philobdella* spp. **Crop**: A major section of the digestive system adapted for the storage of blood or invertebrate body fluids. Typically with one or more pairs of caeca, but acaecate in most Erpobdellids. Also called stomach. **Crop caeca**: Paired diverticula (pouches) of the crop. The last pair (post-caeca) typically extends to XIX/XX in blood-sucking leeches and acaecate in most Erpobdellids. Also called gastric caeca. **Denticles**: Small dentiform processes on the jaws of Hirudinids and Haemadipsids. Denticles typically are in one row (monostichodont) (such as *Hirudo* spp. or *Macrobdella* spp.) or two rows (distichodont) (such as some species of *Philobdella* or *Haemopis*). **Digitate processes**: Approximately 30 or 60 retractable digitiform papillae along the caudal sucker inner margin in *Actinobdella*. Generally retracted in preserved specimens. **Discoid head**: Anterior somites and oral sucker expanded, circular and demarcated from the body with a nuchal (neck) constriction, disciform—as in *Placobdella montifera* and *Placobdella nuchalis*. **Distichodont**: see denticles. **Diverticula (diverticulum—sing.)**: A blind pouch or sac that extends out from the crop or intestine. See also caeca, crop caeca. **Ejaculatory duct**: Paired ducts that run from the epididymis (or sperm sacs in some species) to the male atrium. Arrangement and location of ejaculatory ducts is an important species identification character, especially in some Erpobdellids. Also called preatrial loops. **Epididymis**: Large paired, sperm storage ducts (sometimes coiled) connecting to ejaculatory ducts or sperm sacs (in some Gnathobdellids). Also called seminal vesicle. **Eyes**: Photoreceptors of the dorsal cephalic (head) region that are formed from a number of light-sensitive cells backed by a pigment cup. Eyes are used as higher-level identification characters as they vary in number and arrangement. Also called ocelli or eyespots. **Furrow**: Narrow groove between two annuli (body rings). **Ganglia (ganglion—sing.)**: Enlarged sections of the ventral nerve cord made up of concentrations of neural cells. Leeches have 34 ganglia [six coalesced ganglia in the cephalic region (called brain, nerve ring, pharyngeal ganglionic mass, supraesophageal ganglionic mass, or anterior ganglionic mass), 21 free body ganglia, and seven coalesced ganglia in the caudal region (called posterior ganglionic mass or subesophageal mass)]. Ganglia are given in Roman numerals (i.e., first ganglion

after anterior ganglionic mass is VII). **Gnathous**: The presence of jaws in the pharynx cavity, as in the Hirudinidae. The opposite is agnathus. **Gonopores**: External openings of the male and female reproductive systems, located on the anterior midbody ventral surface. The male pore is larger and anterior to the less conspicuous female pore, however, in a few species, the male and female gonopores are fused into a single pore. **Integument**: The outer layers of protective covering comprised of an epidermis blanketed by an elastic cuticle (with epicuticular projections). **Internal ridges**: See pharynx folds. **Intestine**: Section of the digestive system where digestion and absorption of ingested blood or invertebrate body tissue occurs. **Intestinal caeca**: Paired diverticula (pouches) of the intestine. There are typically four pairs of intestinal caeca in Glossiphoniids, caecate in Piscicolids, and acaecate in Arhynchobdellids. **Jaws**: Cutting apparati (that resemble half circular saw blades) with numerous denticles that typically occur in threes in the mouth cavity of most Hirudinids and Haemadipsids. Jaws are arranged with one median dorsal and the other two ventrolateral, and create a tripartite incision. **Lateral ocelli**: Eyespots found on the lateral margin of the urosome in some Piscicolids, such as *Cystobranchus meyeri.* **Metamere**: see somite. **Metameric**: The division of the body into a series of similar or identical repeating units (e.g., segments or somites). **Metameric dots, spots, patches, or prominences**: Metamerically (segmentally) repeating external dorsal pigment patterns or structures. **Monostichodont**: see denticles. **Mouth**: A medium to large opening on the entire ventral surface of the oral sucker of Arhynchobdellids with rounded lips around the edges. **Mouth pore**: A small opening on the ventral surface of the oral sucker of Rhynchobdellids where a proboscis is protruded and retracted. Located either in the center or the anterior rim of the oral sucker. Also called proboscis pore. **Mycetomes**: Structures (generally paired) in blood-feeding Rhynchobdellids that are located in the esophageal region and harbor symbiotic microflora, which aide in blood digestion. **Neural annulus**: The annulus that contains the ganglion of each somite internally and the metameric sensory organs or sensillae externally. It is the middle annulus in three or five annulate somites. Also called sensory annulus. **Nephridia (nephridium—sing.)**: Metameric excretory organs, opening to the outside via small pores of the body called nephridiopores. **Nuchal plate**: see scute. **Ocelli (ocellus—sing.)**: Photoreceptor cells found on the cephalic, caudal or lateral margins of the body of certain leeches. **Oculiform spots**: see caudal ocelli. **Esophagus**: Narrow duct where ingested blood or invertebrate body fluids pass from the pharynx or proboscis to the crop. May contain mycetomes or esophageal organ in some blood-feeding species. **Oral sucker**: The attachment or suction device found at the anterior end of the leech and contains the mouth or mouth pore. Also called anterior sucker or cephalic sucker. **Oviduct**: Paired ducts that run from the ovisacs to the female gonopore. **Ovisacs**: Specialized coelomic sacs that produce and store eggs. **Papillae**: Protrusible sensory organs that are typically on the dorsal surface, either scattered or metamerically arranged. **Pedicel**: A narrow stalk of annuli supporting the caudal sucker in some leeches (e.g., *Placobdella pediculata*), also called a peduncle. **Penis**: Protrusible organ for transfer of sperm in Hirudinids and Haemadipsid Gnathobdellids. Not present in Rhynchobdellids and Erpobdellids, which transfer sperm via spermatophores (the male atrium is protrusible like a penis in some *Theromyzon* species). **Pharynx**: Anterior muscular section of the digestive system, following the mouth and anterior to the esophagus. **Pharynx folds**: Internal muscular ridges of the pharynx of *Haemopis* species. Also called internal ridges or pharynx pods. **Pigment**: A dorsal or ventral cutaneous structure of color found in chromatophores (typical colors: brown, black, red, green, or blue). **Post-caeca**: The last pair of caeca in the crop. Also called posterior crop caeca. **Posterior sucker**: The attachment or suction device found at the posterior end of the leech. Also called the caudal sucker. **Proboscis**: A modified muscular, tubular protrusible pharynx with a blunt tip and triradiate lumen. Used for feeding by Rhynchobdellids (Glossiphoniidae and Piscicolidae) via insertion into the outer integument of an animal. **Pulsatile vesicles**: Hemispherical extensions of the coelomic system along the lateral body margins of some Piscicolids (e.g., *Cystobranchus* spp. and *Piscicola* spp.). They rhythmically pulsate and function as respiratory organs. **Rays**: A pigmented pattern on the caudal sucker of some Piscicolids. **Salivary glands**: Numerous spherical salivary cells (consisting of a cell soma and elongated ductule) that are either scattered throughout the anterior portion of the body (diffuse) or aggregated in discrete masses (compact), and aid in the ingestion of blood or invertebrate body fluids by secreting salivary chemicals. **Scute**: Dark brown chitinous structure on the dorsal nuchal (neck) region of some *Helobdella* species including *Helobdella stagnalis*. Also called nuchal scute or dorsal plaque. **Segment**: see somite. **Sensillae**: Metameric sensory structures located on the integument of the neural annulus, which provide chemo- and/or mechanoreception. Also called segmental receptors. **Somite**: A serially repeated body segment that corresponds with one ganglion in the central nervous system. All leeches have 34 somites which correspond to 34 ganglia in the nervous system. Somite numbers are given in Roman numerals. Also called segment or metamere. **Spermatophore**: A packet of spermatozoa enclosed in a capsule that is used in Rhychobdellids and Erpobdellids to transport sperm to another adult by hypodermic implantation of the ventral or dorsal body surface (typically the clitellar region in some species).

Sperm sac: Bulbous, muscular paired sperm-storage structure in Hirudinid leeches. Size and arrangement with epididymis are an important species identification character in *Haemopis*. **Stomach**: see crop. **Teeth**: see denticles. **Testisacs**: Specialized coelomic sacs that produce and store spermatozoa. May occur in pairs or grape-like clusters. **Trachelosome**: Narrow, cylindrical neck region (comprised of six somites) in some Piscicolids. **Tubercles**: Large papillae. **Urosome**: Thick, flat mid-body region (comprised of 12 somites) in some Piscicolids. **Vagina**: Enlargement of the female gonopore where the penis is introduced in Hirudinid copulation. **Vas deferens**: Ducts that run anteriorly to form the large epididymis (seminal vesicle). **Vas efferens**: Short ducts that connect the testisacs to the vas deferens on each side of the body. **Velum**: A transverse flap of tissue separating the buccal cavity from the mouth (oral-opening cavity) in Arhynchobbdellids.

MATERIAL PREPARATION AND PRESERVATION

Leeches can often be studied when they are alive and this can provide information on reproduction, feeding, etc., but preserved specimens, dissections, permanently stained slides, and serial sections may be required to identify some species. Colors and patterns should be noted before leeches are preserved because the chromatophores can be dissolved or altered during the preservation process. Slides that have been prepared without stains may need to be cleared to determine eye number and placement.

Specimens will contract when placed into fixatives. It is best to first narcotize the leeches and then, once relaxed, they can be placed into the fixative. Narcotizing and relaxing leeches can be problematic but the following methods have been used successfully:

1. Add drops of 95% ethanol slowly to the water containing the leech, gradually increasing the concentration for about 30 min until movement ceases. When the leech is limp and no longer responds to touch, pass it between the fingers to straighten it and to remove the excess mucus.
2. Add carbonated water or bubble in CO_2 until movement of the leech stops. Straighten the leech out on a slide and slowly add warm 70% ethanol and a few drops of glacial acetic acid until covered.
3. Add a drop or two of 6% nembutal until movement stops and then straighten the leech on a slide.

Relaxed leeches should be fixed in 5%–10% buffered formalin for at least 24 h depending on the size of the individuals. For molecular analyses, specimens should be placed directly into 95% ethanol. Leeches should be kept in 70%–75% ethanol for long-term preservation storage (colors will be bleached out over time). Larger specimens should be injected with formalin to preserve the internal organs. Leeches should be flattened for whole-mount slide preparations by carefully placing the specimens between two glass slides and adding additional weights if necessary. Staining with Semichon's acetocarmine, clearing in methyl salicylate, and mounting in Canada balsam or Damar balsam have shown good results. Fleming's or Bouin's fixatives can be used for histological preparations with specimens being stained in Mayer's paracarmine, borax carmine, or Hams' hematoxylin for 12–94 h and then destained in 1% HCl-70% ethanol and neutralized in a 1% NH_4OH-70% ethanol solution. Once stained, specimens can be counterstained in fast green or eosin and then dehydrated in progressively higher concentrations of ethanol, cleared in methyl salicylate, and mounted in a neutral-pH mounting medium.

Body measurements used in the key for piscicolinae are derived from a mathematical model of leech body form described by Epshtein (1983), Bielecki (1993, 1994, 1997), and Bielecki & Epshtein (1994, 1995). In this model, the leech body is presented in the form of two ellipses (suckers) and six trapeziums between the ellipses (anterior body part—trachelosome—two trapeziums; posterior body part—urosome—four trapeziums). Transverse sections through the trachelosome and the urosome are considered as two ellipses.

The computer model was constructed using the following 29 parameters. (1–4) Parameters describing the form of the anterior sucker: C_1, horizontal diameter; C^1_1, vertical diameter; R_1, length of anterior part of sucker; M_1, length of posterior part of sucker. (5–12) Parameters describing the form of the trachelosome: d_1, width at sucker junction; d_2, width at outline narrowing; d_3, width at border with urosome; D_1, largest width of trachelosome; N_1, largest height of trachelosome; S_1, height of first trapezium; S_2, height of second trapezium; $L_1 = (S_1 + S_2)$, length of trachelosome. (13–25) Parameters describing the form of the urosome: width at places of outline distortion (bases of consecutive trapeziums); d_4, base of first trapezium; d_5, base of second trapezium; d_6, base of third trapezium; d_7, base of fourth trapezium (width at sucker junction); D_2, largest width of urosome; N_2, largest height of urosome; $L_2 = (S_3 + S_4 + S_5 + S_6)$, urosome length (height of consecutive trapeziums); S_3, height of first trapezium; S_4, height of second trapezium; S_5, height of third trapezium; S_6, height of fourth trapezium; K_1, distance from d_3 to D_2; K_2, distance from D_2 to d_7. (26–29) Parameters describing

the form of posterior sucker: $C^1{}_2$, horizontal diameter; C_2, vertical diameter; M_2, length of anterior part of sucker; R_2, length of posterior part of sucker. The 19 body proportion indices (invariants) are as follows:

Index describing L/D_2, relative body length (1).

Indices describing anterior sucker: (2) $C^1{}_1/d_1$, ratio of horizontal diameter of sucker to trachelosome width at sucker junction; (3) $C^1{}_1/D_1$, ratio of horizontal diameter of sucker to greatest width of trachelosome; (4) R_1/M_1, ratio of dorsal part of sucker to its ventral part; (5) $C^1{}_1/C_1$, ratio of horizontal diameter of sucker to its vertical diameter.

Indices describing trachelosome: (6) L_1/D_1, ratio of trachelosome length to its greatest width; (7) D_1/N_1, ratio of greatest trachelosome width to its greatest height; (8) S_1/S_2, index describing position of greatest width of trachelosome.

Indices describing urosome: (9) L_2/D_2, ratio of urosome length to its greatest breadth; (10) D_2/N_2, ratio of greatest urosome width to its greatest height; (11) K_1/K_2, ratio describing position of greatest width of urosome.

Indices describing posterior sucker: (12) $C^1{}_2/d_7$, ratio of horizontal diameter of sucker to urosome width at sucker junction; (13) $C^1{}_2/D_2$, ratio of horizontal diameter of sucker to greatest body height; (14) R_2/M_2, ratio of dorsal part of sucker to its ventral part; (15) $C^1{}_2/C_2$, ratio of horizontal diameter of sucker to its vertical diameter.

Indices describing relations between urosome and trachelosome: (16) L_2/L_1, ratio of urosome length to trachelosome length; (17) D_2/D_1, ratio of greatest width of urosome to greatest width of trachelosome; (18) N_2/N_1, ratio of greatest height of urosome to greatest height of trachelosome.

Index describing proportions of suckers: (19) $C^1{}_2/C^1{}_1$, ratio of horizontal diameter of posterior sucker to horizontal diameter of anterior sucker.

KEYS TO LEECHES

Annelida: Clitellata: Hirudinida: Orders

1 Mouth a small pore on ventral surface of anterior sucker through which a muscular pharyngeal proboscis can be protruded; no jaws or teeth ..... **Rhynchobdellida [p. 495]**

1′ Mouth large, occupying the entire cavity of anterior sucker; no protrusible proboscis; jaws with teeth either present or absent ..... **Arhynchobdellida [p. 499]**

Annelida: Clitellata: Hirudinida: Rhynchobdellida: Families

1 Body margins do not have digitiform branchiae 2

1′ Body with lateral digitiform branchiae (gills) ..... Ozobranchidae, one genus: ***Ozobranchus*** **[p. 495]**

2(1) Body flattened dorsoventrally and much wider than head; body not cylindrical; not differentiated into two body regions; anterior (oral) sucker ventral, more or less fused to body and narrower than body; body never divided into anterior trachelosome and posterior urosome; eggs in membranous cocoons and young brooded on ventral surface of parent; one, two, three, or four pairs of eyes; no oculiform eye spots on posterior sucker; segments three-annulate (a1, a2, a3) ..... **Glossiphoniidae [p. 495]**

2′ Body cylindrical and usually long and narrow; body sometimes divided into a narrow anterior trachelosome and a wider posterior urosome (*Myzobdella*); anterior (oral) sucker expanded and distinct from body; zero, one, or two pairs of eyes; pulsatile vesicles along the lateral margins present (*Piscicola* and *Cystobranchus*) or absent; seven or more annuli per segment (except *Myzobdella reducta* which is three-annulate); oculiform eye spots sometimes present on posterior (caudal) sucker; no brooding of cocoons or young; parasitic primarily on fishes ..... **Piscicolidae [p. 496]**

Annelida: Clitellata: Hirudinida: Rhynchobdellida: Ozobranchidae: *Ozobranchus*: Species

1 Eleven pairs of digitate branchiae (gills) present along margins of body; anterior annulus of biannulate mid-body segments larger and bear branchiae 2

1′ Five pairs of digitate branchiae (gills) present along margins of body ..... *Ozobranchus margoi* (Apathy, 1890)

2(1) Abdominal region with triannulate segments; gills with 4–7 branches ..... *Ozobranchus jantseanus* Oka, 1912

2′ Abdominal region with biannulate segments ..... *Ozobranchus shipleyi* Harding, 1909

Annelida: Clitellata: Hirudinida: Rhynchobdellida: Glossiphoniidae: Genera

1 Proboscis short and not armed with hooked prominences 2

1′ Proboscis long and armed with three hooked prominences near anterior tip ..... *Ancyrobdella* Oka, 1917 [Japan]

2(1) Four pairs of eyes 3

2′ Zero, one, two or three pairs of eyes; a series of paired accessory eyes sometimes present along body 4

3(2) Four pairs of eyes on paramedian lines of segments II–V; body very soft ..... *Theromyzon* Philippi, 1867

3′ Buccal pair of eyes at lateral margin of segment V on a2; remaining three pairs of eyes in two subparallel rows ..... *Oosthuizobdella* Sawyer, 1986

4(2) Midbody segments biannulate (at least dorsally) 5

4′ Midbody segments triannulate 7

5(4) Seven pairs of crop caeca; cocoons attached to substrates 6

5′ Six pairs of crop caeca; biannulate midbody segments; cocoons attached to ventral surface of parent ..... *Baicaloclepsis* Luken & Epshtein, 1959

6(5) Eyes lacking or two pairs ..... *Torix* Blanchard, 1893

6′ Eyes one pair ..... *Mooreotorix cotylifer* (Blanchard, 1898)

7(4) One pair of eyes, distinctly separated 8

7′ Two or three pairs of eyes 9

8(7) Gonopores separated by two annuli; crop caeca six simple unbranched pairs ..... *Batracobdella* Viguier, 1879

8′ Gonopores separated by one annulus; one pair of eyes, distinctly separated or separated by at least the diameter of one eye; proboscis pore (mouth) within anterior sucker and clearly not on rim ..... *Helobdella* Blanchard, 1896

9(7) Nine or more pairs of crop caeca 10

9′ Fewer than nine pairs of crop caeca 11

10(9) Eyes two pairs; 11 pairs of crop caeca ..... *Hemiclepsis* Vejdovsky, 1884

10′ Eyes three pairs with last two pairs separated by two annuli; nine (rarely seven) pairs of crop caeca ..... *Paraclepsis* Harding, 1924

11(9) Three pairs of eyes distinctly separated 12

11′ Two pairs separated either by less than diameter of one eye, touching, or coalesced 13

12(11) First pair of eyes closer together than succeeding two pairs, i.e., eyes arranged in triangular pattern; no papillae; male and female ducts open into a common gonopore; little pigmentation; generally amber-colored; length 10 mm ..... *Alboglossiphonia* Lukin, 1976

12′ Eyes equidistant in two paramedian rows; dorsum with papillae on annulus a2 in six longitudinal rows; pair of paramedial stripes on dorsum and ventrum; seven pairs of crop caeca; gonopores separated by two annuli; length 25 mm ..... *Glossiphonia* Johnson, 1816

13(11) Two annuli between gonopores 14

13′ One to one and a half annuli between gononpores ..... *Parabdella* Autrum, 1936

14(13) Two distinct pair of eyes; dorsum with longitudinal brown lines; seven pairs of crop caeca; papillae absent; length 20 mm ..... *Batracobdelloides* Oosthuizen, 1984

14′ Male and female gonopores separated by two annuli; two pair of eyes (one pair large and one pair small); eyes close together or confluent; body usually papillated; seven pairs of crop caeca; bifurcated ovisacs ..... *Placobdella* Blanchard, 1893

Annelida: Clitellata: Hirudinida: Rhynchobdellida: Piscicolidae: Genera

1 Prostatic glands on atrium, vector tissue and spermatheca absent, eyes and eye spots poorly developed or absent 2

1′ Prostatic glands on atrium, vector tissue and spermatheca present, eyes and eye spots well developed 3

2(1) Posterior sucker very small, its horizontal diameter distinctly smaller than or equal to the largest urosome width; respiratory vesicles large, spherical, semispherical or conical ..... ***Limnotrachelobdella*** **[p. 497]**

2′ Posterior sucker large or very large, its horizontal diameter distinctly larger than the largest urosome width; respiratory vesicles fairly small, fine or nearly invisible ..... *Taimenobdella amurensis* (Epshtein, 1964)

3(1) Conducting strands do not connect ovaries with bursa 4

3′ Conducting strands connect ovaries with bursa ..... *Cystobranchus mammillatus* (Malm, 1863)

4(3) Female gonopore on clitellum invisible, located in spermatheca opening; oviducts cross vector tissue 5

4′ Female gonopore on clitellum visible, located beyond spermatheca opening; oviducts do not cross vector tissue and enter female gonopore anterior to it 6

5(4) Posterior sucker medium-sized, body covered with fine tubercles; bursa short; conducting strands and oviducts run together ..... ***Caspiobdella*** **[p. 497]**

5′ Posterior sucker small, body smooth; bursa longer; conducting strands and oviducts separate *Acipenserobdella volgensis* (Zykoff, 1903)

6(4) Spermatheca opening located behind gonopores 7

6′ Spermatheca opening located between gonopores ..... ***Italobdella*** **[p. 497]**

7(6) Copulatory area surrounds gonopores and spermatheca opening 8

7′ Copulatory area surrounds spermatheca opening 9

8(7) Oviducts enter vector tissue; six pairs of testes; esophageal diverticles present ..... *Pawlowskiella stenosa* Bielecki, 1997

8′ Oviducts enter female gonopore anterior to vector tissue; five pairs of testes; esophageal diverticles absent ..... ***Codonobdella*** **[p. 497]**

9(7) Copulatory area well developed, enters first urosome somite; body length >15 mm ..... ***Piscicola*** **[p. 498]**

9′ Copulatory area poorly developed, not entering first urosome somite; body length <15 mm ..... ***Baicalobdella*** **[p. 499]**

Hirudinida: Rhynchobdellida: Piscicolidae: *Limnotrachelobdella*: Species

1 Respiratory vesicles spherical or semispherical, 11 pairs 2

1′ Respiratory vesicles conical, 10 pairs ..... *Limnotrachelobdella taimeni* Epshtein, 1957

2(1) Somite three- or six-annulate, divided by additional grooves (as a result the number of annuli may reach 14) 3

2′ Somite five-annulate, annuli very distinct ..... *Limnotrachelobdella okae* (Moore, 1924)

3(2) Respiratory vesicles round, horizontal diameter of posterior sucker larger than half of the largest width of urosome; large leeches, length to 45 mm ..... *Limnotrachelobdella sinensis* (Blanchard, 1896)

3′ Respiratory vesicles semispherical, horizontal diameter of posterior sucker smaller than half of the largest width of urosome; medium-sized leeches, length to 18 mm ..... *Limnotrachelobdella turkestanica* Stschegolew, 1912

Hirudinida: Rhynchobdellida: Piscicolidae: *Caspiobdella*: Species

1 Posterior sucker horizontal diameter equal to largest urosome width, tubercles poorly developed, situated on anterior and posterior parts of body 2

1′ Posterior sucker horizontal diameter 1.5 times urosome width, whole body covered with distinct tubercles ..... *Caspiobdella tuberculata* Epshtein, 1966

2(1) Mid-body somite 14-annulate; eye-like spots on posterior sucker 3

2′ Mid-body somite seven-annulate; posterior sucker eye-like spots absent ..... *Caspiobdella hadzi* (Sket, 1985)

3(2) Body coloration not bright (greenish, gray, etc.); dorsal median line a wide light streak, ventral side poorly colored ..... *Caspiobdella caspica* (Selensky, 1915)

3′ Body coloration bright, contrasting, dorsal side light with dark dotted streaks in paramedian lines; ventral side dark gray ..... *Caspiobdella fadejewi* (Epshtein, 1961)

Hirudinida: Rhynchobdellida: Piscicolidae: *Italobdella*: Species

1 Body length to 21.1 mm; anterior sucker with large white "spectacles"; trachelosome and urosome dorsal coloration distinct brown, black, yellow and white melanophores arranged as white transverse segmental spots ..... *Italobdella ciosi* Bielecki, 1993

1′ Body length to 5.9 mm; anterior sucker with pigmented, band; trachelosome and urosome dorsal coloration indistinct with black melanophores present as very fine dots, slightly concentrated in lateromedial lines ..... *Italobdella epshteini* Bielecki, 1997

Hirudinida: Rhynchobdellida: Piscicolidae: *Codonobdella*: Species

1 Body length to 27 mm; body covered with numerous fine papillae; trachelosome/urosome division indistinct; body laterally with transverse, dark brown or black streaks; ejaculatory ducts long, considerably protruding beyond ganglion four ..... *Codonobdella truncata* Grube, 1873

1′ Body length 2.7–3.4 mm; body smooth, with no papillae; trachelosome/urosome division distinct; coloration uniform, no dark streaks; ejaculatory ducts short, reaching ganglion five ..... *Codonobdella zelenskiji* (Finogenova & Snimschikova, 1991)

Hirudinida: Rhynchobdellida: Piscicolidae: *Piscicola*: Species

1 Body cylindrical or nearly so; ratio of urosome greatest width D_2 to its greatest height N_2: $D_2/N_2 \geq 1$ to 1.5 2

1′ Body flattened; ratio of urosome greatest width D_2 to its greatest height N_2: $D_2/N_2 \geq 1.8$ to 3.3 8

2(1) Posterior sucker $C^1{}_2$ horizontal diameter much larger than the greatest urosome width D_2: $C^1{}_2/D_2 \geq 1.5$ to 2.2 3

2′ Posterior sucker C12 horizontal diameter equal to or smaller than the greatest urosome width D_2: $C^1{}_2/D_2 \leq 1$ 4

3(2) Relative body length L/D_2 from 20 to 23; coloration uniform, brown melanophores round, with no processes; posterior sucker without radial streaks and without concavity, resembling a horse hoof; annulation distinct; crop and posterior crop caecum of six diverticula; seminal vesicles reaching testes one, ejaculatory ducts between ganglia four and five, gently bent; ovaries reaching testes one ..... *Piscicola borowieci* Bielecki, 1997

3′ Relative body length L/D_2 from 10 to 13; coloration not uniform, brown and black melanophores stellate, most often form segmental cross-like pattern; posterior sucker with radial streaks and a concavity; annulation indistinct; crop and posterior crop caecum of five diverticles; seminal vesicles reaching testes two, ejaculatory ducts reach ganglion four; ovaries reaching testes two, their ends between testes one intertwined ..... *Piscicola geometra* (Linnaeus, 1758)

4(2) Gonopores separated by two annuli 5

4′ Gonopores separated by more than two annuli 6

5(4) Anterior sucker $C^1{}_1$ width equal to greatest width of trachelosome D_1: $C^1{}_1/D_1 = 1$; crop and posterior crop caecum of four diverticles, secondarily divided; ejaculatory ducts to ganglion five, bent more than four times, seminal vesicles multiply bent, over 10 times; ovaries reaching testes one, not intertwined apically; body to 12.7 mm long ..... *Piscicola witkowskii* Bielecki, 1997

5′ Anterior sucker $C^1{}_1$ wider than greatest width of trachelosome D_1: $C^1{}_1/D_1 > 1$; crop and posterior crop caecum of three diverticles, further undivided; ejaculatory ducts between ganglia four and five, seminal vesicles arcuate; ovaries reaching testes two, apically intertwined; body to 56 mm long ..... *Piscicola annae* Bielecki, 1997

6(4) Mid-body somite four-annulate 7

6′ Mid-body somite of more than four annuli 8

7(6) Coloration gray without segmental spots; five pairs of testes ..... *Piscicola elishebae* Bielecki, 1997

7′ Coloration brown with bright segmental spots; six pairs of testes ..... *Piscicola siddalli* Bielecki, Cios, Cichocka, & Pakulicka, 2012

8(1) Mid-body somite seven-annulate 9

8′ Mid-body somite 14-annulate 10

9(8) Posterior sucker C12 horizontal diameter much larger than the greatest body width D2; C12/D2 from 2.4 to 3.0; copulatory area circular; spermatheca opening at the level of the first pair of respiratory vesicles; crop and posterior crop caecum of two diverticles of equal width; ejaculatory ducts between ganglia three and four; vector tissue circular; parasite of catfish ..... *Piscicola fasciata* Kollar, 1842

9′ Anterior and posterior suckers horizontal diameter subequal; C12/C11 from 1.1 to 1.3; division into trachelosome and urosome distinct; D2/D1 from 2.4 to 2.6; posterior sucker C12 horizontal diameter distinctly smaller than greatest body width D2; $C12/D2 < 1$; copulatory area triangular; spermatheca opening anterior to first pair of respiratory vesicles; crop and caecum posterior crop of three diverticles of unequal width; ejaculatory ducts reach ganglion four; vector tissue elliptical; parasite of trout, grayling, and rheophilous cyprinids ..... *Piscicola respirans* Troschel, 1850

10(9) Mid-body somite of 14 annuli of equal length 11

10′ Mid-body somite of 14 annuli of unequal length 12

11(10) Body abbreviated, relative length $L/D_2 < 6.5$; dorsal with a light streak, its margins diffuse in trachelosome posterior part; anterior and posterior sucker relatively circular; gonopores separated by five annuli; ejaculatory ducts reach ganglion 4, multiply bent; ovaries long, reaching testes two ..... *Piscicola margaritae* Bielecki, 1997

11′ Brown and white melanophores uniformly spaced, brown from four stripes along the lines internally and externally paramedially, intermittent white melanophores in the form of transverse stripes, crop and caecum posterior crop of two diverticles of equal width, ratio of urosome greatest width to trachelosome largest width ≤ 1.9 $D_2/D_1 < 1.9$ ..... *Piscicola burresoni* Bielecki, Cichocka, Światek, & Gorzel, 2013

12(10) Mid-body somite with two groups of annuli 13

12′ Mid-body somite with more than two groups of annuli 14

13(12) Annulus six longer than the remaining ones. Body short, strongly flattened, its relative length $L/D_2 = 7.0$, anterior and posterior suckers elliptical, gonopores separated by four annuli, ejaculatory ducts reach ganglion 5, making regular semi-circle toward trachelosme sides ..... *Piscicola brylinskae* Bielecki, 2001

13′ Annuli 2, 6, and 11 longer than the remaining ones. Horizontal diameter $C^1{}_1$ smaller than the greatest width of trachelosome D_1, anterior sucker very small elliptical $C^1{}_1/C_1 < 1$, horizontal diameter of posterior sucker $C^1{}_2$ equal to body height D_2, $C^1{}_2/D_2 = 1$, division into trachelosome and urosome very poorly marked $D_2/D_1 < 2$. Brown and black melanophores form wide segmental transverse streaks, intermittent with narrow white streaks, crop and posterior crop caecum of five diverticles ..... *Piscicola pojmanskae* Bielecki, 1997

14(12) Three groups of annuli of different length 15

14′ Four groups of annuli of different length 17

15(14) Trachelosome/urosome division obvious, $D_2/D_1 > 2$ 16

15′ Trachelosome/urosome division obscure, D_2/D_1 from 1.1 to 1.4; anterior and posterior suckers round, their horizontal and vertical diameter equal; $C^1{}_1/C_1$ and $C^1{}_2/C_2 = 1$; horizontal diameter of posterior sucker $C^1{}_2$, distinctly larger than the greatest body width D_2, $C^1{}_2/D_2 > 1$; ejaculatory ducts reach ganglion five; wide, seminal vesicles classically U-shaped, at level of testes 1, ovaries wide, sac-shaped ..... *Piscicola jarai* Bielecki, 1997

16(15) $C^1{}_1$ horizontal diameter larger than greatest trachelosome width D_1, round $C^1{}_1/C_1 = 1$; posterior sucker $C^1{}_2$ horizontal diameter smaller than body height D_2, $C^1{}_2/D_2 < 1$; division into trachelosome and urosome obvious, $D_2/D_1 > 2$; brown and black melanophores evenly distributed, crop and caecum posterior crop of four diverticles ..... *Piscicola niewiadomskae* Bielecki, 1997

16′ Anterior and posterior suckers horizontal diameter subequal, $C^1{}_2/C^1{}_1$ from 1.1 to 1.3; trachelosome/urosome division distinct, D_2/D_1 from 2.4 to 2.6; posterior sucker horizontal diameter $C^1{}_2$ distinctly smaller than greatest body width D_2, $C^1{}_2/D_2 < 1$; black melanophores large with long processes and brown pigment cells smaller, without processes, not forming segmental crosses; posterior sucker without radial streaks or streaks obscure; papillae absent; copulatory area circular; ejaculatory ducts reach ganglion four, five times bent; ovaries long, reaching testes two; vector tissue elliptical; seminal vesicles multiply bent ..... *Piscicola pomorskii* Bielecki, 1997

17(14) Anterior and posterior suckers horizontal diameter unequal, $C^1{}_2/C^1{}_1$ from 1.4 to 1.5; trachelosome/urosome division indistinct, D_2/D_1 from 1.9 to 2.1; posterior sucker horizontal diameter $C^1{}_2$ larger than greatest body width D_2, $C^1{}_2/D_2 > 1$; dark gray melanophores without processes forming pattern of segmental crosses, on posterior sucker radial, dark, wide and narrow white streaks; papillae very numerous; copulatory area elliptical, ejaculatory ducts reach ganglion four, once bent, ovaries short, reaching testes one, vector tissue triangular, seminal vesicles as straight transverse rods ..... *Piscicola kusznierzi* Bielecki, 1997

17′ Anterior and posterior suckers palaform, horizontal diamter less than vertical, $C^1{}_1/C_1$ and $C^1{}_2/C_2 < 1$; trachelosome/urosome division distinct, (D_2/D_1) from 1.8 to 2.1; posterior sucker horizontal diameter $C^1{}_2$, distinctly smaller than greatest body width D_2, $C^1{}_2/D_2 < 1$; ejaculatory ducts reach beetwen ganglion four and five; narrow, seminal vesicles ampulliform, located anterior to testes one, ovaries narrow and cylindrical ..... *Piscicola wiktori* Bielecki, 1997

Hirudinida: Rhynchobdellida: Piscicolidae: *Baicalobdella*: Species

1 Anterior sucker horizontal diameter equal to trachelosome greatest width; posterior sucker calyxiform, connected eccentrically, its horizontal diameter equal to half the urosome largest width; body smooth or with barely discernible tubercles on mid annuli ..... *Baicalobdella torquata* (Grube, 1871)

1′ Anterior sucker horizontal diameter < greatest trachelosome width; posterior sucker disk-shaped when unattached, connected centrally, its horizontal diameter < half of urosome largest width; annuli with fine tubercles ..... *Baicalobdella cottidarum* Dogiel & Bogolepova, 1957

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Families

1 Five pairs of eyes arranged in an arch on segments II–VI with the third and fourth pairs of eyes separated by one annulus; body elongate; jaws (except the agnathan Orobdellidae) with denticles (teeth) either present or absent; pharynx short 2

1′ Zero, three, or four pairs of eyes in separate labial and buccal groups; body elongate; no jaws (agnathus), myognaths may have stylets or may lack stylets 3

2(1) Myognaths without stylets; testisacs small and very numerous; pharynx about one-third of body length ..... **Erpobdellidae [p. 500]**

2′ Myognaths typically with stylets; testisacs few; may have have dorsal gastropore; postcephalic eyes may be present ..... **Salifidae [p. 503]**

3(1) Jaws present, with or without denticles; nine or 10 pairs of testisacs arranged metamerically 4

3′ Jaws lacking; with or without ventral gastropore at XIII or XIV; multiple testisacs per segment; ovisacs short and globular ..... Orobdellidae, one genus: ***Orobdella*** **[p. 504]**

4(3) Jaws with one row (monostichodont) of teeth; No pharyngeal ridges terminating independently between jaws 5

4′ Jaws with two rows (distichodont) of teeth; Pharyngeal ridges terminating independently between jaws ..... **Praobdellidae [p. 505]**

5(4) Posterior sucker elliptical and prehensile (able to grasp or wrap around substrates); auricles (ear-like flaps) may be present at base of posterior sucker; ocular areola present on dorsal surface near eyes ..... **Haemadipsidae [p. 505]**

5′ Aquatic or amphibious; posterior sucker circular; lacking auricles next to posterior sucker; lacking ocular areola; skin moist ..... **Hirudinidae [p. 506]**

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Erpobdellidae: Genera

1	Somites of the mid-body homonymously subdivided in annuli of equal width	2
1′	Somites of the mid-body heteronymously subdivided in annuli of unequal width	5
2(1)	Male and female genital pores are separated by 2.5−3 annuli	3
2′	Male and female genital pores are separated by 4−5 annuli, genital pores usually situated in furrows	***Erpobdella*** (in part)
3(2)	Genital pores separated by three annuli; male genital pore situated in furrow	4
3′	Genital pores separated by 2.5 annuli; male genital pore situated on annulus, female genital pore in furrow; most with dorsal dark pattern, sometimes reduced, yellow spots always visible (more visible on dark pattern specimens); genital atrium cornua short, not spirally coiled	***Erpobdella*** (in part)
4(3)	Annuli sharply keeled; dorsal yellowish median stripe (in adults sometimes reduced to anterior body); genital atrium cornua long with double spirally coiled loops; large leeches up to 140 mm in length	*Fadejewobdella quinqueannulata* (Lukin, 1929)
4′	Annuli rounded; dorsally one pair of dark longitudinal stripes, numerous dark spots; genital atrium with short cornua; small to medium-sized leeches up to 45 mm in length	***Erpobdella*** (in part)
5(1)	Mid-body somites are quinqueannulate, only one annulus broadened (sometimes this annulus, rarely more annuli, is subdivided by a shallow furrow), sometimes only very slightly	6
5′	Mid-body somites subdivided into eight or more annuli, usually 2−3 broadened and 5−7 narrow	10
6(5)	Dorsal surface unicolored, without dark patterning; caudal sucker width variable (reduced or reaching up to body diameter)	7
6′	Dorsal surface with dark patterning, caudal sucker small to large but narrower than the maximum body diameter	8
7(6)	Caudal sucker reduced to a small lamella; female genital pore on broadened annulus; genital pores usually separated by 2.5 annuli; body color reddish-white to violet	*Archaeobdella esmonti* Grimm, 1876
7′	Caudal sucker disciform; genital pores separated by two or three annuli	***Dina*** (in part)
8(6)	Body yellowish brown or yellowish, with dorsal irregular dark patches and ventral light yellowish color; eyes absent; genital pores separated by 2.5−3 annuli	***Erpobdella*** (in part)
8′	Dorsal surface with dark longitudinal stripes in pairs	***Dina*** (in part)
9(4)	Dorsal surface without bright spots	10
9′	Dorsal surface with bright spots	***Trocheta*** (in part)
10(9)	Dorsal surface with one pair or more of dark longitudinal stripes	11
10′	Dorsal surface without dark longitudinal paramedian stripes	***Trocheta*** (in part)
11(10)	Genital pores separated by less than six annuli	12
11′	Genital pores separated by six−nine annuli; large leeches to 140 mm, living up to 250 mm	***Trocheta*** (in part)
12(11)	Genital pores separated by two full annuli (may be slightly subdivided); paramedian stripes always well separated	13
12′	Genital pores separated by 3−5 annuli	***Trocheta*** (in part)
13(12)	Four dorsal dark longitudinal stripes dorsally; ovisacs long, not curled	***Trocheta*** (in part)
13′	Dorsally one pair of dark paramedian stripes; ovisacs short, strong curled	***Dina*** (in part)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Erpobdellidae: *Erpobdella*: Species

1	Male and female genital pores are separated by 2.5−3 annuli	2
1′	Male and female genital pores are separated by 4−5 annuli, genital pores usually situated in furrows	3
2(1)	Genital pores separated by three annuli; male genital pore situated in furrow; annuli rounded; dorsally one pair of dark longitudinal stripes, numerous dark spots; genital atrium with short cornua; small to medium-sized leeches up to 45 mm in length	*Erpobdella vilnensis* (Liskiewicz, 1925)
2′	Genital pores separated by 2.5 annuli; male genital pore situated on annulus, female genital pore in furrow; most with dorsal dark pattern, sometimes reduced, yellow spots always visible (more visible on dark pattern specimens); genital atrium cornua short, not spirally coiled	*Erpobdella octoculata* (Linnaeus, 1758)
3(2)	Dorsally unicolored grayish or brownish to black	4
3′	Dorsally with dark pattern	5
4(3)	Vas deferens without praeatrial-loop extending to the previous ganglion; dorsally unicolored grayish to brownish	*Erpobdella quaternaria* (Moore, 1930)

4′ Vas deferens with praeatrial-loop extending to the previous ganglion; dorsally unicolored grayish to black, sometimes with a median light stripe; mouth opening small ..... *Erpobdella testacea* (Savigny, 1822)

5(3) Dorsal surface median with a dark longitudinal stripe; head region elongated ..... *Erpobdella monostriata* (Lindenfeld & Pietruszynski, 1890)

5′ Dorsal surface without a dark longitudinal stripe; head region with a dark neck band; praeclitellar region with reticulated dark pattern, postclitellar region unicolored; mouth opening wide ..... *Erpobdella nigricollis* (Brandes, 1900)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Erpobdellidae: *Dina*: Species

The *Dina ohridiana* species complex consists of species very difficult to separate, and includes: *Dina ohridana* Sket, 1968, *D. lepinja* Sket & Šapkarev, 1986, *D. silvesta* Sket, 1989, *D. krilata* Sket, 1989, *D. eturpshem* Sket, 1989, *D. profunda* Šapkarev, 1990, *D. kuzmani* Šapkarev, 1990, and *D. lyhnida* Šapkarev, 1990. All the species in this complex are found in or in the vicinity of Lake Ohrid.

1 Mid-body somites are quinqueannulate, only one annulus broadened (sometimes this annulus, rarely more annuli, is subdivided by a shallow furrow), sometimes only very slightly broadened 2

1′ Mid-body somites subdivided into eight or more annuli: usually 2−3 broadened and 5−7 narrow; dorsally one pair of dark paramedian stripes; ovisacs short, strongly curled ..... *Dina krasensis* (Sket, 1968)

2(1) Dorsal surface without yellowish or whitish spots 3

2′ Dorsal surface with numerous yellowish or whitish spots obviously visible 14

3(2) Female genital pore always situated behind the broadened annulus, most in the furrow broadened/narrow annulus, sometimes this pore is shift caudad; genital pores are separated by 3−4 annuli 4

3′ Female genital pore situated on broadened annulus or in furrow in front of broad annulus; genital pores separated by 1.5 or 2−3 annuli 5

4(3) Genital pores separated by three or 3.5−4 annuli; coloration grayish, yellow to pinkish and brownish or red, often with a darker pigmentation; some with a very small caudal sucker ..... *Dina ohridana* species complex [endemic to Lake Ohrid and adjacent areas]

4′ Troglobiont, pure white; eyes are absent; genital pores separated by three annuli; ovisacs very short, extended only to next ganglion ..... *Dina ratschaensis* Kobakhidze, 1958 [Georgia]

5(3) Dorsal surface unicolored, without dark pattern; caudal sucker variable (reduced or reaching the maximum body diameter or narrower) 6

5′ Dorsal surface dark patterned; caudal sucker small to large but narrower than the maximum body diameter 7

6(5) Troglobiont, pure white; both genital pores situated in furrows and separated by three annuli; caudal sucker large, equal to maximum body diameter; body surface smooth, without papillae; eyes absent; ovisacs very long, extending ~8−9 somites ..... *Dina absoloni* Johansson, 1913 [western Balkans]

6′ Dorsally whitish to grayish; genital pores in furrows, separated by two annuli; caudal sucker obviously narrower than the maximum body diameter ..... *Dina concolor* (Annandale, 1913)

7(5) Dorsal surface with dark longitudinal stripes in pairs 8

7′ Troglobiont or troglophilic; body yellowish brown or yellowish, dorsally with irregular dark patches and ventrally light yellowish color; eyes absent; genital pores separated by 2.5−3 annuli ..... *Erpobdella borisi* Cichocka, Bielecki, Kur, Pikula, Kilikowska & Biernacka, 2015 [Iran]

8(7) Female genital pore usually on broadened annulus, male genital pore in furrow; two full annuli in front of broadened annulus; genital pores separated by more than two annuli; ovisacs elongated two somites posterior to female genital pore 9

8′ Female genital pore in furrow anterior of broadened annulus; genital pores separated by two full annuli; ovisacs various 9

9(8) Female genital pore usually in shallow furrow on broadened annulus; genital pores separated by 2.5 annuli; medium-sized leeches up to 55 mm in length ..... *Dina lineata lineata* (O. F. Müller, 1774)

9′ Female genital pore always situated on b6, but the position on the annulus is variable; small-sized, reaching a maximum 30 mm in length ..... *Dina lineata lacustris* Sket, 1968

10(9) Mouth opening wide, cranial sucker upper lip not elongated; dorsal surface brighter with visible markings 11

10′ Mouth opening small, upper lip of the cranial sucker elongated; dorsal surface dark, paramedian stripes only slightly darker ..... *Dina montana* Sket, 1968

11(10) Caudal sucker obviously narrower than maximum body diameter; mid-dorsal stripe with a brighter and darker parts lacking; ovisacs curled 12

11′	Caudal sucker slightly narrower than the maximum body diameter; anterior dorsal surface medially with one bright stripe bordered by two wide, dark grayish areas; posterior body with one dark median and two dark paramedian longitudinal stripes; ovisacs curled only posteriorly ..... *Dina sketi* Grosser & Pešić, 2014
12(11)	Ovisacs extend beyond first somite ganglion after female genital pore; dorsal dark paramedian stripes always visible; western Balkans 13
12′	Ovisacs reaching to first somite ganglion after female genital pore, and curled in their entirety; medium to large-sized leeches with a bright mid-dorsal stripe, sometimes one pair of dark paramedian stripes are visible ..... *Dina farsa* Grosser & Pešić, 2008 [Iran]
13(12)	Broadened annulus not or only very slightly subdivided, other annuli not subdivided; eyes reduced, only single eyes may be visible; small leech up to 27 mm in length (preserved); ovisacs extend to fourth somite after female genital pore ..... *Dina prokletijaca* Grosser & Pešić, 2016
13′	All annuli apart from the broadened annuli may be subdivided; eight eye pairs visible (single eyes could be reduced); body length to 50 mm or more; ovisacs extend to third somite after female genital pore ..... *Dina dinarica* Sket, 1968
14(2)	Genital pores separated by 2.5 or less annuli 15
14′	Genital pores separated by three annuli; male genital pore in furrow; three annuli anterior to broadened annulus; dorsal surface with yellow or whitish spots and dark stripes; dorsally with numerous inconspicuous papillae; ovisacs extending to fourth somite posterior to female genital pore, and curled posteriorly ..... *Dina latestriata* Neubert & Nesemann, 1995 [Lake Prespa]
15(14)	Male genital pore situated on annulus; genital pores separated by 1.5 or 2.5 annuli 16
15′	Both genital pores situated in furrow, separated usually by two annuli; ovisacs curled or not 17
16(15)	Genital pores separated by 1.5 (to 1.75) annuli; postclitellar region annuli tending to subdivide into more annuli; ovisacs extend to fourth somite posterior to female genital pore; vasa deferentia obviously longer than ovisacs and extend to sixth somite posterior to female genital pore; dorsal surface with or without dark paramedian stripes ..... *Dina mauchi* Nesemann, 1995
16′	Genital pores separated by 2.5 annuli; fifth annulus very slightly broadened; annuli not subdivided into annuli; ovisacs and vasa deferentia extending to fifth ganglion posterior to female genital pore; dorsal surface usually with dark paramedian stripes ..... *Dina japonica* (Pawlowski, 1962)
17(15)	Ovisacs not curled 18
17′	Ovisacs curled posteriorly, extending to third somite posterior to female genital pore; vasa deferentia extending to seventh somite posterior to female genital pore ..... *Dina orientalis* Grosser, Nesemann & Pešić, 2011
18(17)	Genital atrium coruna short, extending to somite border or to broadened annulus of previous somite 19
18′	Genital atrium coruna long, extending to anterior of atrium body ganglion 21
19(18)	Dorsal surface not concave, without laterocaudal fringes, distinctive lateral keels are present; ovisac posterior portions ventral to vasa deferentia 20
19′	Body exceptionally flattened dorsally and rounded ventrally, dorsal surface concave with very prominent laterocaudal fringes; ovisacs extend dorsally to vasa deferentia ..... *Dina maroccana* Nesemann & Neubert, 1994
20(19)	Bright mid-dorsal stripe absent, color usually dark red-brown to black; broadened annulus always obviously subdivided into two smaller annuli, with a tendency to divide further annuli; small to medium-sized leeches ..... *Dina punctata* Johansson, 1927
20′	Bright mid-dorsal stripe present, color dark grayish on bright-brownish background; broadened annulus not or only slightly subdivided, no tendency for annuli to divide; medium to large-sized leeches ..... *Dina minuoculata* Grosser, Moritz & Pešić, 2007
21(18)	Ovisacs and vasa deferentia extending to seventh somite ganglion posterior to female genital pore 22
21′	Ovisacs extending to seventh somite ganglion posterior to female genital pore; vasa deferentia one somite shorter ..... *Dina apathyi* Gedroyć, 1916
22(21)	Cephalic region paramedian stripes present, yellow spots small, head region dark; atrium cornua slightly wider than long ..... *Dina stschegolewi* (Lukin & Epshtein, 1960)
22′	Cephalic region paramedian stripes absent, yellow spots large, united into transverse stripes; atrium cornua longer than wide ..... *Dina pseudotrocheta* Grosser & Eiseler, 2008

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Erpobdellidae: *Trocheta*: Species

1	Dorsal surface without bright spots 2
1′	Dorsal surface with bright spots 12
2(1)	Dorsal surface with one or more pairs of dark longitudinal stripes 3
2′	Dorsal surface without dark longitudinal paramedian stripes 8
3(2)	Genital pores separated by less than six annuli 4
3′	Genital pores separated by 6–9 annuli; large leeches to 140 mm, living up to 250 mm ..... *Trocheta subviridis* Dutrochet, 1817

4(3) Genital pores separated by 3–5 annuli 5

4′ Genital pores separated by two full annuli (may be slightly subdivided); paramedian pair of stripes always separated 6

5(4) Genital pores separated by 4–5 annuli; dorsal site with one faint median light stripe, bordered by two dark longitudinal stripes ..... *Trocheta falkneri* Nesemann & Neubert, 1996

5′ Genital pores separated by three to four annuli; dorsal surface median dark stripes dense side by side, median light stripe is absent ..... *Trocheta dalmatina* Sket, 1968

6(4) Four dorsal dark longitudinal stripes; ovisacs long, not curled 7

6′ One pair of dorsal dark paramedian stripes; ovisacs short, curled ..... *Dina krasensis* (Sket, 1968)

7(6) Body ground color black; lateral keels prominent ..... *Trocheta africana* Nesemann & Neubert, 1994

7′ Body ground color light brown, lateral keels not prominent ..... *Trocheta tunisiana* Ben Ahmed, Bielecki, Cichocka, Tekaya, Gorzel & Harrath, 2013

8(2) Dorsal surface smooth, without conspicuous papillae; genital pores separated by two broadened full annuli (sometimes slightly subdivided into three or four narrow annuli) 9

8′ Dorsal surface rough, with numerous, conspicuous papillae; genital pore separation variable; very large leeches, living specimens over 200 mm 11

9(8) With visible eyes (sometimes typical number of eight reduced); annulation with clear two or three broadened annuli (sometimes split by shallow furrows into additional narrow annuli) and five to seven narrow full annuli; cranial sucker upper lip obviously elongated; body slender 10

9′ Without eyes; mouth opening wide, cranial sucker upper slightly elongate; postclitellar region posterior third exceptionally broadened; annulation primary quinqueannulate with one visible broadened full annulus; broadened full annulus split by shallow furrows into two or three annuli, the subsequent narrow annulus split by a shallow furrow into two annuli; typically troglobiont ..... *Trocheta vignai* (Minelli, 1978)

10(9) Ovisacs extend to third or fourth somite posterior to female genital pore, not curled posteriorly; small mountain streams, caves ..... *Trocheta taunensis* Grosser, 2015

10′ Ovisacs extend to second or third somite posterior to female genital pore, curled posteriorly ..... *Trocheta cylindrica* Örley, 1886

11(8) Accessory genital pores lateral of the male genital pore small but visible; male and female genital pore in furrow, separated by two broadened annuli (by three annuli, if the second broadened annuli slightly subdivided) ..... *Trocheta haskonis* Grosser, 2000

11′ Without accessory genital pores: male genital pore on broadened full annulus, in shallow furrow; female genital pore shifted on third narrow annulus; genital pores separated by 3.5 narrow annuli ..... *Trocheta danastrica* Stschegolew, 1938

12(1) Dorsally always with one pair of faint paramedian stripes, usually with a bright or dark median field; lateral keels absent in the last third of the body ..... *Trocheta riparia* Nesemann, 1993

12′ Dorsally without paramedian stripes, a narrow dark median line mostly visible; posterior third of body with lateral keels, in adults broadened; vasa deferentia extend to seventh somite ganglion posterior to female genital pore; ovisacs to sixth somite ganglion posterior to female genital pore ..... *Trocheta pseudodina* Nesemann, 1990

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Salifidae: Genera

1 Ventral accessory copulatory pore absent 2

1′ Two ventral accessory copulatory pores present ..... ***Barbronia*** **[p. 504]**

2(1) Dorsal gastropore absent 3

2′ Dorsal gastropore present in posterior part of somite XIV ..... *Scaptobdella horsti* Blanchard, 1897

3(2) Eyes absent behind somite IV 4

3′ One or several pairs of eyes present behind somite IV ..... ***Salifa*** (in part)

4(3) Stylets parallel to body axis 5

4′ Mid-body somites nine-annulate; stylets transverse to body axis ..... *Sinodontobdella kinzelbachi* (Nesemann, 1995)

5(4) Male gonopore in somite XI/somite XII 6

5′ Male gonopore not in somite XI/somite XII 7

6(5) Female gonopore in somite XII/somite XIII ..... *Mimobdella japonica* Blanchard, 1897

6′ Female gonopore situated at posterior part of somite XIII, i.e., in somite XIII b5/b6 or in middle of somite XIII b6 ..... ***Odontobdella*** (in part)

7(5) Female gonopore in somite XII/somite XIII ..... ***Odontobdella*** (in part)

7′ Female gonopore not in somite XII/somite XIII ..... ***Salifa*** (in part)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Salifidae: *Barbronia*: Species

1	Dorsal surface without irregular blackish mottles	2
1′	Dorsal surface with irregular blackish mottles; eyes hardly detectable in adult	*Barbronia nepalensis* Nesemann & Sharma, 2007
2(1)	Dorsal surface reddish to dark red-brown in life; eyes detectable in adult	*Barbronia weberi* (Blanchard, 1897)
2′	Dorsal surface dark olive-green to ocher in life; eyes hardly detectable in adult	*Barbronia shillongensis* Nesemann, 2007

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Salifidae: *Salifa*: Species

1	One or several pairs of eyes present behind somite IV	2
1′	Eyes absent behind somite IV	4
2(1)	Mid-body somites six-annulate	3
2′	Eyes in 5−7 pairs, one large pair on somite III or IV, then each small pair situated laterally at posterior margin of a2 of each somite in somites V−IX; mid-body somites five-annulate	*Salifa lateroculata* (Kaburaki, 1921)
3(2)	Eyes in three pairs, one large pair on somite III, then each small pair situated dorsolaterally at posterior margin of a2 of each somite in somites V and VI; gonopores separated by five annuli	*Salifa biharensis* Nesemann, Sharma & Sinha, 2004
3′	Eyes in seven pairs, one large pair on III, then each two small pairs on a2 of each somite of somites V and VI, and each four small pairs on b4 of each somite of somites VII−X, gonopores separated by six annuli	*Salifa hainana* Yang, 1996
4(1)	Mid-body somite basically six-annulate, subdivided into eight-annulate; male gonopore in somite XI b4/b5; female gonopore in middle of somite XII b4	*Salifa yunnanensis* (Yang, 1997)
4′	Mid-body somite basically five-annulate, subdivided into six-annulate; male gonopore in somite XII b2/a2; female gonopore in somite XIII b1/b2	*Salifa zhejiangica* (Yang, 1996)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Salifidae: *Odontobdella*: Species

1	Male gonopore not in somite XI/somite XII	2
1′	Male gonopore in somite XI/somite XII	*Odontobdella blanchardi* (Oka, 1910)
2(1)	Mid-body somite basically six-annulate, subdivided into 11-annulate	*Odontobdella krishna* Nesemann & Sharma, 2012
2′	Mid-body somite basically seven-annulate, subdivided into nine-annulate	*Odontobdella polaneci* Nesemann, 1995

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Orobdellidae: *Orobdella*: Species

1	Mid-body somites four-annulate	2
1′	Mid-body somites six- or eight-annulate	11
2(1)	Gonopores separated by more than five full annuli	3
2′	Gonopores separated by less than five full annuli	4
3(2)	Gonopores separated by 1/2 + 5 annuli; gastroporal duct bulbous; atrial cornua developed, ovate	*Orobdella tsushimensis* Nakano, 2011
3′	Gonopores separated by six annuli; gastroporal duct simple tubular; atrial cornua undeveloped	*Orobdella kawakatsuorum* Richardson, 1975
4(2)	Gonopores separated by 1/2 + 4 + 1/2 annuli	5
4′	Body length less than 5 cm; gonopores separated by 1/2 + 4 [+ (<1/2)] annuli; gastroporal duct tubular; epididymides short, in somites XX to XXI; atrial cornua small, ovate	*Orobdella brachyepididymis* Nakano, 2016
5(4)	Gastroporal duct not simple tubular; epididymides present; atrial cornua developed, ovate	6
5′	Gastroporal duct simple tubular; epididymides absent; atrial cornua undeveloped	*Orobdella ketagalan* Nakano & Lai, 2012
6(5)	Gastroporal duct bulbous	7
6′	Gastroporal duct tubular, but bulbous at junction with gastropore; epididymides in somites XVI to XX	*Orobdella esulcata* Nakano, 2010

7(6)	Body length less than 5 cm	8
7′	Body length of mature individuals reaching ~10 cm; epididymides in somites XVI to XVIII	*Orobdella whitmani* Oka, 1895
8(7)	Somite XXV four-annulate	9
8′	Somite XXV three-annulate; epididymides in somites XV to XX	*Orobdella koikei* Nakano, 2012
9(8)	Epididymides occupying more than five full somites	10
9′	Epididymides occupying less than four full somites, in somites XVI to XVIII	*Orobdella masaakikuroiwai* Nakano, 2014
10(9)	Epididymides in somites XIV to XVIII	*Orobdella kanaekoikeae* Nakano, 2017
10′	Epididymides in somites XV to XX	*Orobdella naraharaetmagarum* Nakano, 2016
11(1)	Mid-body somites six-annulate	12
11′	Mid-body somites eight-annulate	17
12(11)	Somite VIII five-annulate; pharynx reaching to somite XVI; gastroporal duct rudimentary; epididymides absent; atrial cornua absent	13
12′	Somite VIII six-annulate; pharynx reaching to somite XIV; gastroporal duct developed; epididymides present; atrial cornua present	14
13(12)	Gonopores separated by eight annuli; rudiment gastroporal duct reaching to somite XVI	*Orobdella dolichopharynx* Nakano, 2011
13′	Gonopores separated by nine annuli; rudiment gastroporal duct reaching to somite XV	*Orobdella shimadae* Nakano, 2011
14(12)	Gonopores separated by 1/2 + 7 + 1/2 annuli	15
14′	Gonopores separated by 8 + 1/2 annuli	16
15(14)	Somite VII four-annulate; epididymides in somites XVI to XIX; pre-atrial loop of ejaculatory ducts absent	*Orobdella ijimai* Oka, 1895
15′	Somite VII five-annulate; epididymides in somites XVI to XVIII; pre-atrial loop of ejaculatory ducts present, extending to anterior of somite XI c9	*Orobdella yamaneae* Nakano, 2016
16(14)	Somite VII four-annulate; gastroporal duct tubular, but bulbous at junction with crop; epididymides in somites XV to XIX	*Orobdella mononoke* Nakano, 2012
16′	Somite VII five-annulate; gastroporal duct bulbous; epididymides in somite XV to XVII	*Orobdella okanoi* Nakano, 2016
17(11)	Gonopores separated by 1/2 + 10 + 1/2 annuli; epididymides in somites XVII to XIX	*Orobdella octonaria* Oka, 1895
17′	Gonopores separated by 1/2 + 11 or 12 annuli; epididymides in somites XV to XVII	*Orobdella nakahamai* Nakano, 2016

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Praobdellidae: Genera

1	Jaws with 3–4 pairs of teeth per jaw	***Myxobdella*** **[p. 505]**
1′	Jaws small without teeth	*Dinobdella ferox* (Blanchard, 1896)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Praobdellidae: *Myxobdella*: Species

1	Mid-body imperfectly five annulate with furrows of unequal depth, forming groups of 2-1-2 or 2-3 rings per segment, color pattern of spots or blotches (no stripe)	2
2′	Mid-body imperfectly five annulate with furrows forming groups of 1-2-2 rings per segment; color pattern with longitudinal mid-dorsal light stripe	*Myxobdella nepalica* Nesemann & Sharma, 2001
2(1)	Body pale gray with irregular dark blotches	*Myxobdella annandalei* Oka, 1917
2′	Body with several series of metameric spots	*Myxobdella sinanensis* Oka, 1925

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Haemadipsidae: Genera

1	Mid-body somites five-annulate	***Haemadipsa*** **[p. 506]**
1′	Mid-body somites four-annulate	*Tritetrabdella taiwana* (Oka, 1910)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Haemadipsidae: *Haemadipsa*: Species

1 Gonopores separated by five full annuli 2

1′ Gonopores separated by two full annuli ..... *Haemadipsa cavatuses* Yang, Mo & Wang, 2009

2(1) Interocular plates of somite IV subdivided 3

2′ Interocular plates of somite IV undivided 6

3(2) Dorsal surface with irregular markings 4

3′ Dorsal surface with longitudinal black stripes 5

4(3) Anus "Y"-shaped; caudal sucker with more than 75 friction rays (71–77) ..... *Haemadipsa yanyuanensis* Liu & Song in Song, Zhang, Tan & Liu, 1977

4′ Caudal sucker with less than 75 friction rays (72–73) ..... *Haemadipsa hainana* Song, Zhang & Tan in Song, Zhang, Tan & Liu, 1977

5(3) Dorsal surface yellowish; furrow pits four or five pairs on somites VIII to XI or XII ..... *Haemadipsa sylvestris* Blanchard, 1894

5′ Dorsal median–paramedian surface multicolored, generally greenish; furrow pits undeveloped ..... *Haemadipsa picta* Moore, 1929

6(2) Ventral surface black or blackish 7

6′ Ventral surface generally brownish 8

7(6) Body blackish; dorsal surface with black stripe; caudal sucker with 66–76 friction rays ..... *Haemadipsa agilis* Moore, 1929

7′ Body grayish; dorsal surface with irregular markings; caudak sucker with 71–72 friction rays ..... *Haemadipsa rjukjuana* Oka, 1910

8(6) Dorsal surface with longitudinal stripe(s) 9

8′ Dorsal and ventral surfaces with black irregular markings; caudal sucker with 72–74 friction rays ..... *Haemadipsa tianmushana* Song in Song, Zhang, Tan & Liu, 1977

9(8) Dorsal surface with single median longitudinal stripe 10

9′ Dorsal surface with several longitudinal stripes 12

10(9) Dorsal median longitudinal stripe black 11

10′ Dorsal median longitudinal stripe yellow; ventral surface with slight irregular markings ..... *Haemadipsa zeylanica* (Moquin-Tandon, 1826)

11(10) Dorsal and ventral surfaces without irregular markings ..... *Haemadipsa montivindicis* Moore, 1929

11′ Dorsal surface with irregular black markings ..... *Haemadipsa qomolangma* Song & Jiang in Song, Zhang, Tan, & Liu, 1977

12(9) Ventral surface without longitudinal stripe 13

12′ Ventral surface with two black longitudinal stripes; caudal sucker with 75 friction rays ..... *Haemadipsa yanbianensis* Tan, Pan, & Feng, 1988

13(12) Dorsal surface with three black longitudinal stripes; furrow pits obvious ..... *Haemadipsa japonica* Whitman, 1886

13′ Dorsal surface with five black longitudinal stripes ..... *Haemadipsa guangchuanensis* Tan, Pan, & Feng, 1988

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Hirudinidae: Genera

1 Jaws monostichodont, well developed or vestigial 2

1′ Jaws distichodont, small or absent ..... ***Haemopis*** **[p. 507]**

2(1) Dorsum with five longitudinal yellow stripes 3

2′ Dorsum with two or four orange or reddish stripes or rows of spots ..... ***Hirudo*** (in part)

3(2) Anterior end wide and round, same as or slightly less than the maximum body width; venter lacking any spots and stripes; jaws well developed with denticles ..... ***Hirudo*** (in part)

3′ Anterior end attenuated, less than half or one-third of maximum body width; venter with two marginal spotted stripes and many spots; jaws vestigial with no denticles ..... *Whitmania laevis* (Baird, 1869)

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Hirudinidae: *Hirudo*: Species

1 Dorsum with two or four orange or reddish stripes or rows of spots 2

1′ Dorsum with five longitudinal yellow stripes; venter lacking any spots and stripes; jaws well developed with denticles ..... *Hirudo nipponia* Whitman, 1886

2(1) Dorsum with narrow longitudinal orange or reddish stripes; venter with dark pattern or unicolored light 3

2′ Dorsum with two broad, diffuse longitudinal orange stripes; venter unicolored greenish to yellow with a pair of black marginal stripes; vagina, a sharply folded, elongated tube; epididymis small, not much larger than ejaculatory bulb ..... *Hirudo verbana* Carena, 1820

3(2) Venter with irregularly arranged and sized black markings or unicolored light 4

3′ Venter black, with metameric pairs of light-colored markings; dorsum with quadrangular metameric or rounded black dots; vagina, an evenly curved tube; epididymis medium-sized, somewhat larger than ejaculatory bulb ..... *Hirudo orientalis* S. Utevsky & Trontelj, 2005

4(3) Dorsum with elongated metameric black spots 5

4′ Dorsum with quadrangular metameric black dots; ventral marginal stripes zigzaged; vagina bulbous, upright and not folded; epididymis massive in relation to ejaculatory bulb ..... *Hirudo troctina* Johnson, 1816

5(4) Dorsum with fusiform black spots on paramarginal stripes; dorsal marginal stripes lacking; ventral marginal stripes straight if present, venter with dark pattern; epididymis massive in relation to ejaculatory bulb; vagina, terminally curved or straight tube ..... *Hirudo medicinalis* Linnaeus, 1758

5′ Dorsum with elongated ellipsoid black spots on paramarginal stripes; dorsal marginal stripes zigzaged; ventral marginal stripes lacking; venter unicolored with irregularly arranged black dots; epididymis medium-sized; vagina evenly curved ..... *Hirudo sulukii* Saglam et al., 2016

Annelida: Clitellata: Hirudinida: Arhynchobdellida: Hirudinidae: *Haemopis*: Species

1 Body pigmentation well developed; eyes present; small jaws present; anus large ..... *Haemopis sanguisuga* (Linnaeus, 1758)

1′ Body unpigmented; eyes lacking; jaws lacking; anus small ..... *Haemopis caeca* Manoleli et al., 1998

2′ Venter darker than dorsum ..... *Haemopis elegans* Moquin-Tandon, 1846

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Subclass Acanthobdella

1 No anterior (oral) sucker, mouth on ventral surface of segment III; no jaws; posterior sucker present consisting of four segments; two pairs of chaetae on five consecutive anterior segments; distal ends of chaetae bent to form hooks (Fig. 12.36); length 22 mm; ectoparasite of salmonids ..... *Acanthobdella peledina* Grube, 1851

1′ First five segments delimited from body and form an anterior sucker; chaetae of the first and second rows and also the outer chaetae of the third row are slender and not bent to form hooks; ectoparasite of whitefish ..... *Acanthobdella livanowi* Epshtein, 1966

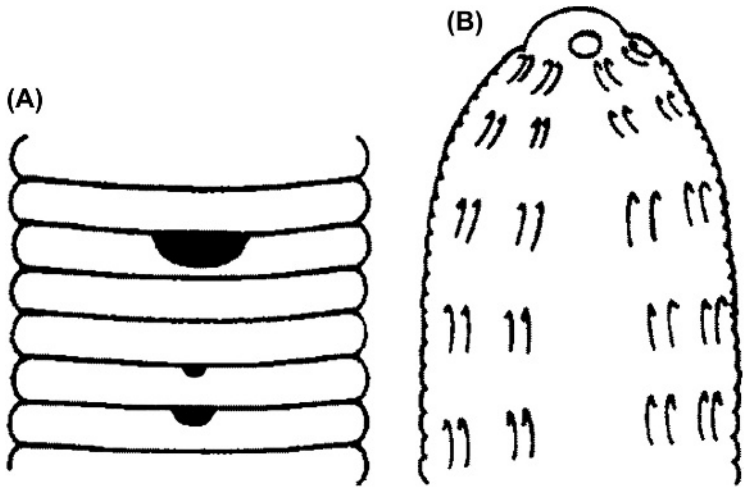


FIGURE 12.36 *Acanthobdella peledina*, ventral view of: (A) the male and female gonopores with a spermatheca; and (B) the anterior view showing the absence of an anterior sucker, the presence of a mouth pore, and five pairs of hooked chaetae.

Class Aphanoneura

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INTRODUCTION

The Aphanoneura are a class of Annelida, with an equivocal relationship with clitellates (oligochaetes and leeches) and no clear affiliation with any of the traditional polychaete groups (Struck & Purschke, 2005; Zrzavý et al., 2009). They comprise two families, Aeolosomatidae and Potamodrilidae, which have been included among the Polychaeta in previous reviews of freshwater annelids (Glasby & Timm, 2008; Glasby et al., 2009). Aeolosomatidae, currently considered Annelida *incertae sedis* (WoRMS, 2012), is the most diverse and abundant aphanoneuran represented in the Palaearctic by three genera: *Rheomorpha* Ruttner-Kolisko, 1955 (one species), *Hystricosoma* Michaelsen, 1926 (one species) and *Aeolosoma* Ehrenberg, 1828 (at least 20 species). The Potamodrilidae is represented in the Palaearctic by a single species, *Potamodrilus fluviatilis* (Lastočkin, 1935.)

LIMITATIONS

The status of *Aeolosoma arenicola* Semernoy, 2004 and *A. singulare* Semernoy, 1982, both endemics from Russia (Lake Baikal), needs to be revised; they are not included in the key.

TERMINOLOGY AND MORPHOLOGY

Compared to most polychaetes, Aeolosomatidae and Potamodrilidae have simplified body plans. Aeolosomatids lack head appendages and parapodial lobes and appendages, and their bodies are highly ciliated. The aeolosomatids have constrictions along the body, giving them a segmented appearance and more often have four bundles of chaetae per segment (usually capillary chaetae, but some may also have sigmoid hooks as well or, more rarely, only hooks). Their body surfaces are brightly colored due to the epidermal gland cells, each one consisting of a vacuole, filled with red, green, blue-green, yellow, or sometimes colorless liquid. The potamodrilids closely resemble the aeolosomatids, but may be distinguished in lacking the colored epidermal glands. In the keys, we follow conventional oligochaete terminology in using roman numerals for segment numbering; segment II represents the first segment with chaetae (= first chaetiger).

MATERIAL PREPARATION AND PRESERVATION

The Aphanoneura should be always identified alive. When fixed they tend to burst and lose most of the taxonomically important structures.

KEYS TO APHANONEURA

Adapted from Van der Land (1971) and Timm (2009). The latter provides illustrations for most of the currently recognized species of Aphanoneura.

Annelida: Aphanoneura: Families

1 Prostomium with uniformly flat ciliated underside, and a pair of lateral ciliated sensory pits; asexual reproduction by paratomy (with development of budding zones) prevailing; mature individuals rare, if present, sperm and eggs develop in different segments, while enlarged paired nephridia serve as male ducts; spermathecae small and irregularly placed; mostly in surface waters ..... **Aeolosomatidae [p. 509]**

1′ Prostomium with flat underside divided into three subsequent fields; no lateral sensory pits; segment number fixed as seven (six of them bearing chaetae (Fig. 12.37 A–C)); no asexual reproduction; unpaired male, female, and spermathecal pore in VI; meiopsammon of rivers ..... Potamodrilidae, one species: *Potamodrilus fluviatilis* (Lastočkin, 1935)
[France. Germany: Weser, Elbe, Lake Stechlin rivers. Lithuania. Poland: Prypec River. Russia: Kaliningrad Region, Don, Moskva, Oka, Volga rivers. Ukraine: Dnieper River]

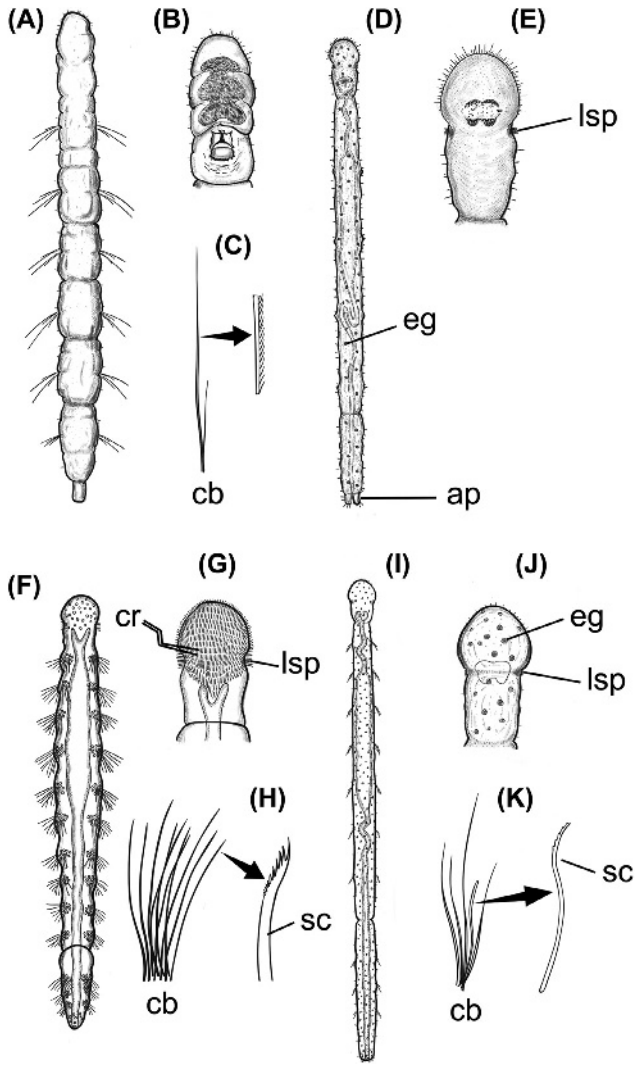


FIGURE 12.37 (A–C) *Potamodrilus fluviatilis*: (A) dorsal view of body; (B) ventral view of anterior end; (C) chaetae; (D and E) *Rheomorpha neizvestnovae*: (D) dorsal view of body; (E) dorsal view of anterior end; (F–H) *Hystricosoma chappuisi*: (F) dorsal view of body; (G) ventral view of anterior end; (H) chaetae; (I–K) *Aeolosoma psammophilum*: (I) dorsal view of body; (J) dorsal view of anterior end; (K) chaetae. *ap*, adhesive appendages; *cb*, chaetal bundle; *cr*, ciliary rows; *eg*, epidermal gland; *lsp*, lateral sensory pit; *sc*, sigmoid chaeta. *(A–E) and (I–K) after Bunke (1967); (F–H) after Pop (1975).*

Annelida: Aphanoneura: Aeolosomatidae: Genera

Adapted from Timm, 2009.

1′ Chaetae present, being either capillary chaetae only, or combined with shorter stiff sigmoid chaetae, both in dorsal and ventral bundles 2

1 Chaetae absent, chaetal bundles replaced by adhesive papillae (Fig. 12.37 D); body ventrally flattened; two posterior terminal adhesive appendices; epidermal glands colorless (Fig. 12.37 E), yellowish, greenish, or absent; asexual reproduction by budding; meiopsammon of lakes, rivers, and springs ..... *Rheomorpha neizvestnovae* (Lastočkin, 1935) [Finland. France: hyporheic water in karstic zones at the French Pyrenees, Lake Léman. Germany: Plöner See, Lake Stechlin, rivers Elbe, Lech, Weser. Italy: Lake Maggiore. Latvia. Lithuania. Poland. Russia: Kaliningrad Region, rivers Volga, Dnieper, Lake Ladoga. Switzerland: Léman, Maggiore. Ukraine: Kaniv Reservoir, Dnieper]

2(1) Dorsal chaetae 5−12 per bundle, arranged in two transverse rows or in an elliptical row, in each bundle; body cylindrical but prostomium flat (Fig. 12.37 F−H); epizoic on crayfish ..... *Hystricosoma chappuisi* Michaelsen, 1926
[Belarus. Bulgaria. Croatia. Czech Republic. Germany. Greece. Hungary. Kosovo. Poland. Romania. Ukraine: Kotlabukh Lake, rivers Udai, Sula]

2′ Chaetae in all bundles in one single row, not arranged in a special way (Fig. 12.37 K); body flat, at least ventrally; free-living..... ***Aeolosoma*** **[p. 510]**

Annelida: Aphanoneura: *Aeolosoma*: Species

1 Bundles of chaetae consist of long, flexible capillary chaetae and short, stiff sigmoid chaetae (the latter often only in the posterior bundles; rarely absent in the first zooid) (Fig. 12.37 K) 2

1′ Sigmoid chaetae completely absent 9

2(1) Sigmoid chaetae smooth or with one row of small teeth near distal end (visible in lateral view, with oil-immersion) 3

2′ Sigmoid chaetae with very thin distal point and two rows of 5−10 relatively large teeth on concave side of distal end, 30−40 µm long; epidermal glands colorless ..... *Aeolosoma travancorense* Aiyer, 1926
[Germany. Latvia. Netherlands. Poland. Portugal. Russia. Slovenia. Ukraine: Dnieper River. Tunisia. Lebanon]

3(2) Large, body width 120−200 µm; capillary chaetae reaching a length of 150−200 µm; sigmoid chaetae 45−70 µm long, with one or more teeth on convex side of distal end or smooth (?) (teeth easily overlooked) 4

3′ Small, body width 50−100 µm; capillary chaetae up to 135 µm long, but mostly considerably shorter; sigmoid chaetae up to 45 µm long, rarely up to 50 µm long 6

4(3) Sigmoid chaetae only in posterior bundles, from V backwards, sometimes only in ventral bundles, but rarely absent in the first zooid 5

4′ Sigmoid chaetae may occur in all bundles, although they are mostly absent in II; epidermal glands green ..... *Aeolosoma leidyi* Cragin, 1887
[France: Lake Léman. Germany. Netherlands. Spain. Switzerland: Lake Léman. Turkey. Iraq: Tigris River and Al-Swaib marshes]

5(4) Epidermal glands orange ..... *Aeolosoma japonicum* Yamaguchi, 1953
[Netherlands: near Leiden. Poland: Konin lakes. Korea. Japan: Hokkaido]

5′ Epidermal glands greenish yellow to olive green ..... *Aeolosoma tenebrarum* Vejdovský, 1880
[Czech Republic. France. Germany: Elbe River. Great Britain. Latvia. Lithuania. Moldova. Netherlands. Poland: Konin lakes. Portugal. Russia: northwestern, central. Spain. Switzerland. Turkey. Ukraine]

6(3) Sigmoid chaetae smooth or with teeth on concave side of distal end 7

6′ Sigmoid chaetae with 5−10 small teeth on convex side of distal end; epidermal glands red (Fig. 12.37 I, J) ..... *Aeolosoma psammophilum* Bunke, 1967
[Germany: River Weser]

7(6) Sigmoid chaetae in dorsal and ventral bundles 8

7′ Sigmoid chaetae only in ventral bundles; ciliated field with typical laterodorsal continuations; epidermal glands orange-red ..... *Aeolosoma evelinae* Marcus, 1944
[Germany. Netherlands]

8(7) Sigmoid chaetae smooth, distal end sharply bent, 28−35 µm long; epidermal glands colorless or absent ..... *Aeolosoma beddardi* Michaelsen, 1900
[Great Britain. China: Chongqing, Jiangsu, Sichuan]

8′ Sigmoid chaetae mostly with two or three very small teeth, but sometimes difficult to see or absent, distal end not sharply bent, ~35 µm long; epidermal glands lemon-colored ..... *Aeolosoma sawayai* Marcus, 1944
[Germany. Poland: Konin lakes]

9(1) Fission-zone after VII to XI 10

9′ Fission-zone after XIV to XVI; large species, body width 150−200 µm; epidermal glands orange-red ..... *Aeolosoma gertae* Marcus, 1944
[Netherlands]

10(9) Capillary chaetae mostly reaching a greater length, being longer than body width, the shortest not resembling sigmoid chaetae 11

10′ Capillary chaetae very short, 25−75 µm long, mostly considerably shorter than body width, the shortest chaetae resembling sigmoid chaetae; small species, body width 50−100 µm; epidermal glands orange-red ..... *Aeolosoma quaternarium* Ehrenberg, 1831
[Croatia. Czech Republic. Denmark. Finland. France. Germany: Elbe River. Great Britain. Italy. Lithuania. Luxembourg. Poland. Russia: central, eastern, northern, northwestern, Kaliningrad Region, Lake Ladoga, Lake Baikal. Ukraine. Iraq: Tigris River]

11(10) Longest capillary chaetae more than 175 µm; body width about 150−300 µm; epidermal glands green or yellow 12

11′ Longest capillary chaetae shorter than 160 μm; body width 40–175 μm 14

12(11) Epidermal glands green; no commissural vessels 13

12′ Epidermal glands yellow; commissural vessels present ..... *Aeolosoma tenuidorsum* Baskin, 1928
[Ukraine: Kharkiv River]

13(12) Body width 200–300 μm; capillary chaetae up to 250 μm long; fission-zone after VII or VIII, rarely after IX; intestine dilated from IV to VI or VII ..... *Aeolosoma viride* Stephenson, 1911
[(?) Belgium. Croatia. Czech Republic. Italy]

13′ Body width 150–200 μm; capillary chaetae up to 400 μm long; fission-zone after IX to XI, mostly after X; intestine dilated from IV to VIII, IX or X ..... *Aeolosoma headleyi* Beddard, 1888
[Austria. China: Hubei, Jiangsu, Sichuan. Croatia. Denmark. (?) Finland. France: Camargue. Germany. Great Britain. Italy. Israel. Japan: Hokkaido. Moldova. Poland: Konin lakes. Russia: central, northwestern. (?) Spain. Turkey.]

14 (11) Refractive epidermal glands colorless or absent 15

14′ Colored epidermal glands present 16

15(14) Small, body width about 80 μm long; fission-zone after VI or VII, rarely after VIII; epidermal glands without satellite cells; capillary chaetae subequal, 50–80 μm, mostly two or three per bundle ..... *Aeolosoma niveum* Leydig, 1865
[Czech Republic. Finland. France: Lake Léman. Germany: Elbe River. Lithuania. Luxembourg. Netherlands. Poland. Russia: central, eastern, northern, northwestern, Lake Baikal. Switzerland: Lake Léman. Ukraine. Japan: Honshu]

15′ Moderately small, body width 80–130 μm; fission-zone after IX to XI, rarely after VIII; epidermal glands with satellite cells; capillary chaetae unequal, up to more than 100 μm long, 3–5 in most bundles ..... *Aeolosoma hyalinum* Bunke, 1967
[France. Germany: River Weser. Netherlands. Mauritania]

16(14) Epidermal glands orange-red 17

16′ Epidermal glands green or yellow 18

17(16) Large, body width more than 100 μm, up to 175 μm; fission-zone after VIII–XII, rarely after VII, mostly after X; capillary chaetae up to 150 μm long, up to 10 per bundle ..... *Aeolosoma litorale* Bunke, 1967
[Finland. Germany: River Weser]

17′ Small, body width 40–100 μm; fission-zone after VI to VIII, mostly after VII; capillary chaetae up to 120 μm long, up to six, rarely up to eight per bundle ..... *Aeolosoma hemprichii* Ehrenberg, 1828
[Austria. Belarus. Belgium. Bulgaria. Croatia. Czech Republic. Denmark. Estonia. Finland. France: Lake Léman. Germany: Lake Stechlin, rivers Elbe, Weser. Great Britain. Ireland. Italy: mainland and Sardinia. Latvia. Luxembourg. Moldova. Netherlands. Poland. Portugal. Russia: Kaliningrad Region, central, northern, northwestern, lakes Ladoga, Baikal. Slovenia. Switzerland: Lake Léman. Mauritania. India: Kashmir. China: Hubei, Jiangsu, Sichuan, Xizang. Japan: Honshu]

18(16) Epidermal glands green or greenish yellow 19

18′ Epidermal glands golden yellow; intestine dilated from III–V ..... *Aeolosoma flavum* Štolc, 1903
[Czech Republic. Germany: Weser River. Poland: Konin lakes]

19(18) Epidermal glands faintly green, with homogeneous contents, without satellite cells; fission-zone after VI or VII ..... *Aeolosoma olivaceum* Bunke, 1967
[France: Camargue. (?) Germany]

19′ Epidermal glands greenish yellow, containing granules and globules, with satellite cells; fission-zone after VII–IX ..... *Aeolosoma variegatum* Vejdovský, 1884
[Czech Republic. Denmark. Estonia. Finland. France: Lake Léman. Germany: Elbe River. Great Britain. Ireland. Italy. Latvia. Lithuania. Luxembourg. Netherlands. Poland. Portugal. Russia: central, northern. Slovenia. Switzerland: Lake Léman. China]

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Class Polychaeta

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INTRODUCTION

Polychaeta is a class of mainly marine and brackish water annelids; recent studies using independent molecular datasets have shown that the class is a catchall for many unrelated groups, and as a consequence is likely to be formally abandoned in the near future. The number of Palaearctic freshwater and inland saline taxa is reduced, comprising only 18 known species and subspecies.

These taxa may be found in habitats ranging from saline seas, water reservoirs, lakes, and karstic environments, to springs, streams, and rivers (Glasby et al., 2009). All

species are benthic, living in both soft and hard grounds, and in the case of *Carazziella spongilla* Sato-Okoshi, 1998, as a symbiont of the freshwater sponge *Spongilla alba* Carter, 1849. Another species, *Protodrilus spongioides* Pierantoni, 1903, is known from a single freshwater aquarium in Naples (Italy), containing specimens of *Petromyzon* Linnaeus, 1758, collected at the nearby Sarno River.

The most abundant Palaearctic family is the Fabriciidae (two genera, five species), followed by the Ampharetidae (one genus, three species), the Nereididae (three genera, three species), and the Serpulidae and Spionidae (two genera, two species each). The Nerillidae, Protodrilidae, and Sabellidae are represented by one species each.

Most species and the genus *Marifugia* are endemic to the Palaearctic. Exceptions include *Ficopomatus enigmaticus* (Fauvel, 1923) and *Alitta succinea* (Leuckart, 1847), two species with a wide distribution as a result of deliberate and accidental introductions. Taxonomic confusion may have also contributed to some perceived wide distributions, as proved to be some case with northern European *Laonome calida* Capa, 2007, previously thought to have been introduced from Australia, but now considered to be introduced from elsewhere and referred to a new species, *L. xeprovala* Bick & Bastrop, 2018. Three species show disjunct distributions, namely *Troglochaetus beranecki* Delachaux, 1921, *Streblospio gynobranchiata* Rice & Levin, 1998, and *Namanereis hummelincki* (Augener, 1933). In the first case the amphi-Atlantic distribution was tentatively explained based on a Pangean radiation of the group (Glasby & Timm, 2008).

Two Palaearctic areas are considered especially interesting in that they are home to narrow-range endemics: Lake Baikal and its tributaries, and the Ponto-Caspian region (Glasby & Timm, 2008). However, the taxa occurring there—species of *Hypania* Ostroumov, 1896 and *Manayunkia* Leidy, 1859—are in need of revision, so this idea needs confirmation.

LIMITATIONS

The genus *Hypania* needs to be revised; until this time, we consider *H. kowalewskii* (Grimm, 1876) to belong to *Hypania* rather than *Hypaniola* Annenkova, 1927. *Manayunkia baicalensis hydai* was named by Slastnikov (1940) for specimens collected in lakes Khaseynto and Yambuto (Gyda River basin, northern Siberia, Russia), but it was never formally described. Thus, the subspecies is a *nomen nudum* and therefore is not included in the key. *Manayunkia caspica danubialis* Băcesco, 1948, from the Danube River, comprises the *lapsus calami M. caspica fluviatilis*; in spite of being ill-defined the subspecies is considered to be a synonym of *Manayunkia caspica* Annenkova, 1929. The status of *Fabricia* Blainville, 1828 needs to be revised.

TERMINOLOGY AND MORPHOLOGY

Polychaeta are characterized by having a body formed by multiple small, repeated units (segments) arranged longitudinally along the body. Often the only differentiated segments are the anteriormost (**prostomium**), which may include sensory and feeding appendages, and the posteriormost (**pygidium**), which includes the anus and, often, sensory organs. However, some forms may have the body divided into two or more regions: an anteriormost thorax and a posteriormost abdomen. Most polychaetes have characteristic bundles of chaetae on each segment (one or two on each side); the chaetae often are carried by the parapodia, which are variously well developed and assist with locomotion. Other paired internal and external structures are for feeding (**palps**, **tentacular crown**), sensory (**palps**, **cirri**), protective (**elytrae**), respiratory (**branchiae**), excretory (**nephridia**), or reproductive (**gonopores**) purposes.

Polychaete morphology is extraordinarily diverse, as it corresponds to a group of organisms that are adapted to virtually all marine environments, having also some terrestrial and freshwater representatives.

The protodrilids and the nerillids are interstitial forms; both have a ciliated body, anterolateral palps, and a pygidium with two appendages. The protodrilids are elongate with many segments (more than 20), lack parapodia and chaetae, and usually have a pair of specialized adhesive lobes on the pygidium. In contrast, nerillids are very short with few segments, have both parapodia and chaetae, and the pygidium bears a pair of anal cirri. Simple pigmented eyes may be present in both families.

The nereidids are typical errant polychaetes, with multisegmented, long bodies and a well-developed cephalic region, which bears two bilobed palps, two antennae, tentacular cirri (three or four pairs), and a muscular eversible pharynx equipped with a pair of lateral jaws, multiple accessory denticles (called **paragnaths**), and/or **papillae**; rarely, denticles and papillae are absent. They have parapodia with one dorsal (**notopodial**) and one ventral (**neuropodial**) ramus, each bearing multiple lobes and one or more bundles of chaetae. **Chaetae** are always compound, with short (**falcigerous**) or long (**spinigerous**) blades, but chaetal articulation may be fused in posterior segments in some cases. They also have one pair of pygidial, or anal, cirri. Sexually mature adults (also called **epitokes**) have modified midposterior body segments, which carry enlarged parapodial lobes bearing paddle-shaped chaetae which facilitate swimming. Epitokes are uncommon among freshwater nereidids.

Spionidae have more sedentary habits than nereidids. Their cephalic region is characterized by a prostomium that anteriorly may be rounded, truncate, pointed, or bear a pair of lateral horns, and is elongated posteriorly. A pair of

highly mobile, grooved, tentacular feeding palps (used either to filter particles in the water or to feed on bottom sediments) is always present (but often lost in preserved specimens), and they may also have a median antenna. The parapodia have noto- and neuropodia and lack dorsal and ventral cirri. Branchiae are often associated with the parapodia; they are somewhat flattened and may be simple, laterally ciliated, or carry pinnae or lamellae, and occur all along the body or be restricted to a few anterior segments. The pygidium has highly variable morphologies (paired elongate anal cirri, numerous smaller cirri, lobes, or anal plates). The chaetae are simple capillaries (smooth or limbate), simple hooks with apical teeth, often sheathed, and stout sabre chaetae. Polydorid spionids, including the freshwater *Carazziella* Blake & Kudenov, 1978, have an enlarged fifth segment that carries one or several additional types of chaetae including large spines of different shapes and slender accessory chaetae.

Ampharetidae are clearly sedentary polychaetes, with slightly more modified bodies, having a well-defined segmentation, a thorax with short cylindrical notopodia and ridge-shaped neuropodia (tori) bearing hooked **uncini**, and an abdomen with neuropodia only. They have a small prostomium situated on top of a larger unit consisting of the fused first and second segments, which is surrounded by lateral lips. The ampharetids lack antennae and bear short palps (as slender tentacles inside the buccal cavity, which can be swallowed) and, occasionally, one or two very much larger grooved palps. Dorsal and ventral cirri are absent, but they have up to four pairs of branchiae on anteriormost segments. The pygidium may have many cirri. Chaetae are capillaries in the thoracic notopodia and uncini in the neuropodia. Either slender, peg-like notochaetae and/or notopodial paleae may rarely occur in anterior parapodia, while paired large hooks might occur in place of paleae. The ampharetids are deposit feeders, which gather food particles from the bottom sediments by means of their buccal tentacles. They construct fragile tubes by aggregating mud particles, or less frequently larger sand grains or debris.

Sabellids, serpulids, and fabriciids are tube-dwelling polychaetes with relatively similar morphologies. All have reduced prostomia and an anterior branchial crown, which is thought to be homologous to palps of other polychaetes. They have a ring-shaped peristomium, with or without an anterior collar. Their bodies are clearly segmented and divided into a thorax and abdomen, and their parapodia are usually biramous. Dorsal and ventral cirri, as well as branchiae, epidermal papillae, and pygidial cirri are absent. Sabellids and serpulids may be clearly distinguished by the composition of their tubes: mucose with aggregate sediments in the former (with one single marine exception) and calcareous in the latter. The sabellids have somewhat cylindrical notopodia and neuropodial tori anteriorly; posterior notopodia and neuropodia are tori and short cylinders, respectively, and the chaetae include different types of capillaries, dentate hooks without hoods, and uncini. The sabellids, also known as feather-duster worms, are mostly filter-feeders and use their tentacular crown to trap suspended particles, both for food and to build their tubes. A few species, however, are surface deposit feeders, especially those small taxa living on muddy sediments, which may include most freshwater species. The tentacular crown is also a respiratory organ and the radioles may have photosensitive eyespots, which may also be present on the pygidium in some species. The serpulids have both short, truncate, cylindrical parapodia and tori, which are noto- and neuropodial, respectively, in the thorax, and neuro- and notopodial, respectively, in the abdomen. Their chaetae include differently ornamented capillaries and uncini. In addition to tube differences, the presence of an operculum (a modified radiole) also enables the immediate recognition of serpulids; however, we caution in using this structure alone in a diagnosis as it may be absent in some species, while in others it is very fragile and easily lost in preserved specimens. Serpulids are all filter feeders and have a relevant role as fouling organisms. In contrast, fabriciids are quite similar to sabellids and indeed they were once a subfamily of the latter. In general, fabriciids have a smaller body and separate branchial lobes (comprising the tentacular crown), while sabellids have branchial lobes that are fused mid-dorsally.

MATERIAL PREPARATION AND PRESERVATION

Polychaetes are most easily identified after fixation, although information on coloration, ciliation, etc., which may be useful at the species level, may be lost or obscured. Optimal specimen conditions for morphological observations are achieved through first relaxing the animals using a few grains of $MgCl_2$ or $MgSO_4$ in fresh water for a few minutes to several hours (depending on the group). After relaxation, freshwater polychaetes should be fixed in a 4% formaldehyde solution made by diluting stock formaldehyde (i.e., 40%) 10 times with tap water. After one to a few days, specimens should be washed gently in fresh water and transferred to 70%–80% ethanol for identification, and long-term storage. Alternatively, fixation in osmium tetroxide after relaxing is advisable for observations under scanning electron microscopy.

KEYS TO POLYCHAETA

Adapted from Glasby & Fauchald (2000).

Polychaeta: Families

1 Fifteen body segments or more bearing parapodia and chaetae; macrobenthic forms 2

1′ Thirteen body segments or fewer bearing parapodia and chaetae (if more than 14 segments, then parapodia and chaetae lacking); small interstitial forms..... 7

2(1) Prostomium without paired slender anteriorly directed, anterolateral antennae; jaws absent; compound chaetae absent..... 3

2′ Prostomium with paired slender, anteriorly directed, anterolateral antennae; jaws present (Fig. 12.38 A); compound chaetae present .... **Nereididae [p. 515]**

3(2) Palps not paired, as numerous buccal tentacles or as a tentacular crown; chaetiger five always unmodified; body regionation present; uncini present..... 4

3′ Palps paired, grooved; chaetiger five unmodified or greatly modified (with specialized chaetae as spines of two types); body regionation absent; uncini absent ..... **Spionidae [p. 516]**

4(3) Chaetal inversion present (thoracic uncini in neuropodial position, abdominal uncini notopodial) (Fig. 12.38 B); palps as tentacular crown 5

4′ Chaetal inversion absent; palps as numerous tentacles within buccal cavity (Figs. 12.38 E, F) Ampharetidae, one genus: ***Hypania*** **[p. 516]**

5(4) Thoracic membrane absent; tube otherwise, normally muddy..... 6

5′ Thoracic membrane present (Fig. 12.38 B); tube calcareous ..... **Serpulidae [p. 517]**

6(5) Abdominal uncini rasp-shaped plates, with an elongate manubrium below dentate region ..... **Fabriciidae [p. 517]**

6′ Abdominal uncini rasp-shaped plates or with series of teeth above main fang, but without an elongate manubrium below dentate region ..... Sabellidae, one species: *Laonome xeprovala* Bick & Bastrop, 2018
[Baltic and North Sea coastal and catchment areas including Pärnu Bay, Vistula Lagoon, Kiel Canal, Swedish, Finnish and Latvian coastal waters, Odra and Don Rivers, Netherlands, Elbe estuary, Sea of Azov (Taganrog and Temtyuk Bays). Introduced, but of unknown origin]

7(1) Minute interstitial forms; parapodia present (Fig. 12.38 C); chaetae as simple or compound capillaries; pygidium usually with two anal cirri, without adhesive glands; phreatic and hyporheic caves, wells and springs .... Nerillidae, one species: *Troglochaetus beranecki* Delachaux, 1921
[Austria, Czech Republic, Finland, France, Germany, Hungary, Italy, Poland, Romania, Slovakia, Switzerland]

7′ Slender, elongate interstitial forms; parapodia absent; chaetae absent; pygidium bilobed (deeply furcate, resembling toes) with adhesive glands, anal cirri absent (Fig. 12.38 D) (known only from a freshwater aquarium with *Petromyzon* Linnaeus, 1758) .... Protodrilidae, one species: *Protodrilus spongioides* Pierantoni, 1903
[Italy]

Polychaeta: Nereididae: Genera

1 Parapodia fully biramous in median and posterior region, with lobes and chaetae in both rami; pharynx with paragnaths; four pairs of tentacular cirri..... 2

1′ Parapodia with reduced notopodia, lacking ligules and chaetae, and with a single neuropodial ligule poorly developed; pharynx lacking paragnaths and papillae; three pairs of tentacular cirri (Fig. 12.38 A); wells, springs ..... *Namanereis hummelincki* (Augener, 1933)
[Canary Islands]

2(1) Middle and posterior neuropodia with one homogomph falciger, or a single simple chaeta (fused falciger) (best seen in the posteriormost region of the body); dorsal notopodial ligule subtriangular, similar in size throughout the body .... *Hediste diversicolor* (O.F. Müller, 1776)
[Caspian Sea, Aral Sea (introduced)]

2′ Homogomph falcigers absent; dorsal notopodial ligule markedly elongate and broader on posterior chaetigers .... *Alitta succinea* (Leuckart, 1847)
[Caspian Sea (introduced)]

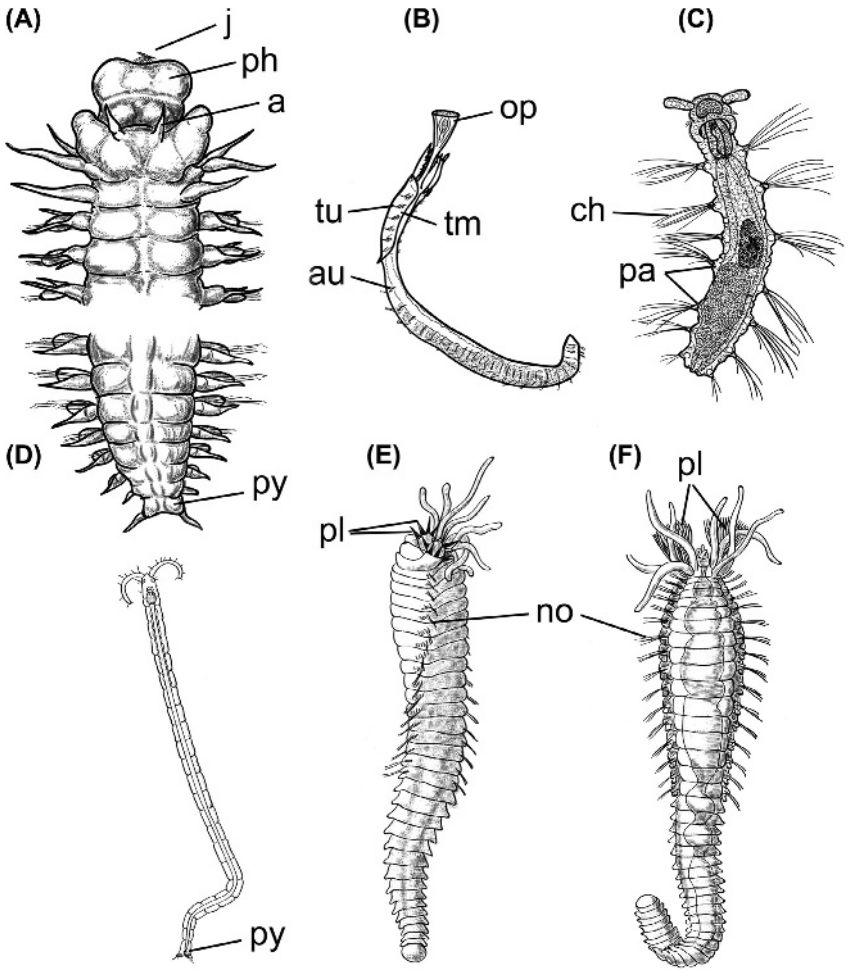


FIGURE 12.38 (A) *Namanereis hummelincki*, head end (upper) and tail end (lower); (B) *Marafugia cavatica* male; (C) *Troglochaetus beranecki*; (D) *Protodrilus* sp.; (E) *Hypania brevispina*; (F) *Hypania invalida*. a, antenna; au, abdominal uncini; ch, chaetae; j, jaw; no, notochaetae; op, operculum; pa, parapodia; ph, pharynx; pl, paleae; py, pygidium; tm, thoracic membrane; tu, thoracic uncini. *(A) after Wesenberg-Lund (1958); (B) after Absolon & Hrabě (1930); (C) after Andrássy (1956); (D) after Paxton (2000); (E–F) after Grube (1860).*

Polychaeta: Spionidae: Genera

1 Chaetiger five greatly modified, with specialized chaetae as spines of two types, first with expanded end, second falcate; branchiae start at chaetiger 6, continuing to middle of body; dorsal folds absent in anterior region of body; symbiontic of the freshwater sponge *Spongilla alba* Carter, 1849 ..... *Carazziella spongilla* Sato-Okoshi, 1998
[Japan]

1′ Chaetiger five without specialized chaetae; a single pair of branchiae on chaetiger 1; chaetiger 2 with dorsal fold .... *Streblospio gynobranchiata* Rice & Levin, 1998
[Volga-Don canal, from Black Sea to Caspian Sea (introduced?)]

Polychaeta: Ampharetidae: *Hypania*: Species

1 Thirteen thoracic uncinigers; prostomium with glandular ridges (or nuchal organs referred to as glandular ridges) 2

1′ Fourteen thoracic uncinigers; prostomium without glandular ridges (or nuchal organs referred to as glandular ridges) .... *Hypania kowalewskii* (Grimm, 1876)
[Caspian Sea, Romania, Russia]

2(1) Between 15–30 long and thin paleae; 16 chaetigers with capillary notochaetae (Fig. 12.38 F) ..... *Hypania invalida* (Grube, 1860)
[Caspian Sea, Russia (Volga, Don (?)), Poland (Odra River), Ukraine (Dnipro, Dnister), River Bug (Ukraine, Belarus, Poland), Danube River (Romania to Germany), Great Britain (Bristol Avon, Severn, Thames, Trent)]

2′ Between 7–10 short and strong paleae; 17 chaetigers with capillary notochaetae (Fig. 12.38 E) ..... *Hypania brevispina* (Grube, 1860)
[Caspian Sea]

Polychaeta: Serpulidae: Genera

Adapted from ten Hove & Kupriyanova, 2009.

1 Operculum with chitinous spines; collar chaetae present, being coarsely serrated and simple ..... *Ficopomatus enigmaticus* (Fauvel, 1923)
[Caspian Sea (invasive)]

1′ Operculum lacking spines; collar chaetae absent (Fig. 12.38 B); caves..... *Marifugia cavatica* Absolon & Hrabě, 1930
[Bosnia and Herzegovina, Croatia, Slovenia, Italy]

Polychaeta: Fabriciidae: Genera

1 Branchial crown with two pairs of pinnulate radioles; ventral filamentous appendages vascularized, unbranched; anterior margin of anterior peristomial ring modified as a thin annulate membrane; thoracic uncini with broad series of equal size teeth above main fang ..... ***Manayunkia***

1′ Branchial crown with three pairs of pinnulate radioles; ventral filamentous appendages absent; anterior margin of anterior peristomial ring collar modified to a wide well-developed lobe; thoracic uncini with unequal size teeth above main fang ..... *Fabricia stellaris caspica* (Zenkewitsch, 1922)
[Turkmenistan]

Polychaeta: Fabriciidae: *Manayunkia*: Species

1 Branchial crown well developed, with 22−104 branchial pinnules; manubrium of abdominal uncini with wide base; mature adults ≤4 mm; fresh water 2

1′ Branchial crown poorly developed, with 12−18 branchial pinnules; manubrium of abdominal uncini with narrow base; mature adults 1.5−4.0 mm; brackish and fresh water ..... *Manayunkia caspica* Annenkova, 1929
[Ponto-Caspian region, Danube River (Romania to Serbia)]

2(1) Branchial crown normally with more than 40 pinnules (up to 104); mature adults usually more than 5−6 mm long; pygidium pointed; at least some segments poorly pigmented; in soft substrata, between 0.8−80 m depth 3

2′ Branchial crown with 22−38 pinnules (occasionally 40−42); mature adults up to 4 mm long (usually 2.5−3.5 mm long); pygidium rounded; all segments well pigmented; on hard substrata (rocks and stones), between 1.5−20 m depth (seldom down to 30 m) ..... *Manayunkia zenkewitschii* Sitnikova, Shcherbakov & Kharchenko, 1997
[Lake Baikal]

3(2) Branchial crown with 40−62 pinnules, rarely more; mature adults up to 8 mm long (usually 5−6 mm); pygidium pointed and elongated; pigment spots mainly on branchial crown and first 5−6 segments; sandy sediments, 0.8−80 m depth ..... *Manayunkia baicalensis* (Nusbaum, 1901)
[Lake Baikal, (?)Amur and Lena basins]

3′ Branchial crown with 72−104 pinnules, rarely less; mature adults up to 13 mm long (usually 9−11 mm); pygidium pointed, but not elongated; pigment spots absent or rarely present on the first two segments; muddy sediments, 2.5−80 m ..... *Manayunkia godlewskii* (Nusbaum, 1901)
[Lake Baikal]

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Chapter 13

Phylum Ectoprocta

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INTRODUCTION

The phylum Ectoprocta is primarily a marine group with over 8000 recognized species and a rich fossil record with many thousands more. The 100 or so bryozoan species known from fresh water would seem to be overshadowed by such a robust family tree. In fact, however, freshwater bryozoans are an important part of the benthic community in lakes, ponds, and rivers worldwide. They filter suspended particles from the water, and their fecal pellets provide nourishment for a wide variety of scavengers. Bryozoans are also significant biofouling organisms that often interfere with the function of irrigation, water treatment, and industrial cooling systems (Wood, 2005a).

LIMITATIONS

This chapter recognizes 33 species of freshwater bryozoans in the Palaearctic region. Many are well known and easily identified, while others are distinguished only by minute and sometimes tentative features. Most of the difficult taxonomic issues occur in the Plumatellidae, which comprises about half the Palaearctic species. Over the past several decades much progress has been made in the taxonomy of the entire group, but many questions remain unresolved.

Freshwater bryozoans are unequally classified among two major groups: (1) the exclusively freshwater class Phylactolaemata, and (2) the mostly marine order Ctenostomata within the class Gymnolaemata. In the Palaearctic region, phylactolaemates are said to be represented by at least 34 species and the ctenostomes by 10 species (Massard & Geimer, 2008). In years to come these numbers will surely be revised. My own current estimate is 29 phylactolaemate species and four ctenosomes.

The soft tissues of bryozoans offer few reliable features for species identification. Hard parts, when they are available, tend to be much more consistent and verifiable. Among freshwater bryozoans, the ctenostomes, with no hard anatomical parts, are often very difficult to identify with certainty. It is not surprising that the species number in this group is relatively low. The traditional taxonomist is forced to rely on such variable features as tentacle counts and gut morphology.

By contrast, phylactolaemate bryozoans have taxonomically useful hard parts in the encapsulated products of asexual reproduction called statoblasts. These provide a wealth of characters, such as relative shapes and dimensions, as well as tiny tubercles and net-like lines that are believed to be species specific. In most cases, the statoblast alone is sufficient to identify a species. In fact, in

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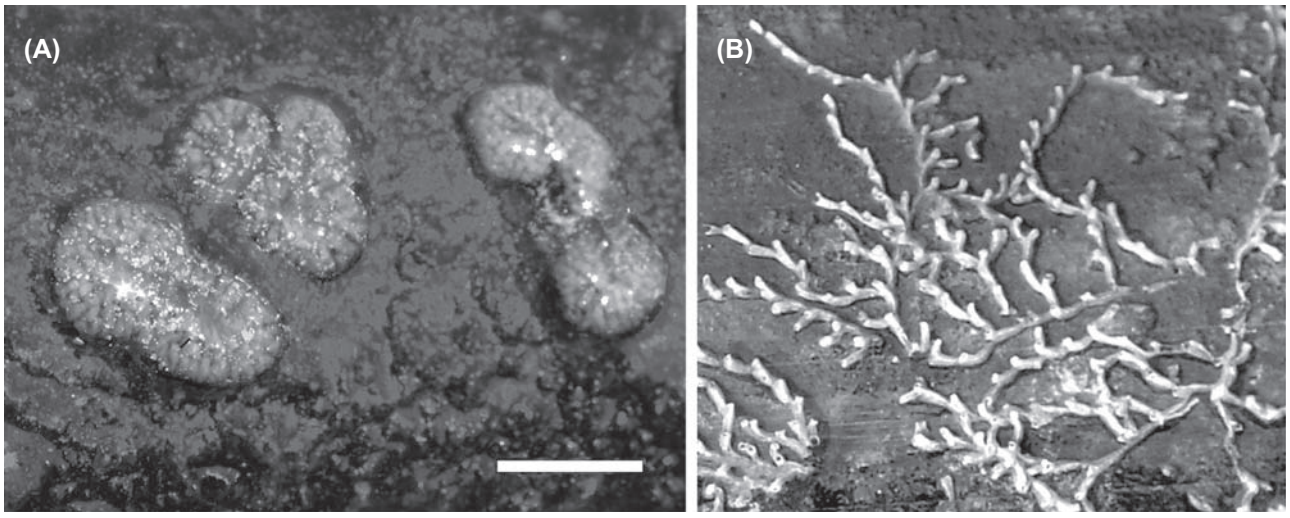


FIGURE 13.1 Two basic morphologies of bryozoan colonies. (A) Globular colonies of *Asajirella gelatinosa*; (B) tubular colonies of *Plumatella bombayensis*. Scale bar = 1 cm.

the absence of statoblasts, many phylactolaemates cannot be positively identified at the species level.

However, even statoblasts have their limitations. The search for ever more elusive taxonomic features has inevitably led to important features being detected only through scanning electron microscopy (SEM). This becomes a challenge to those investigators without access to such an instrument. In the following key I have tried to avoid using characters that rely on SEM examination, but in a few cases it simply was not possible.

The reported species distributions naturally depend on the accuracy of species identification. Our understanding of taxonomically significant features has evolved over many years. Even now the value of floatoblast nodules, for example, is not universally accepted. Partly for this reason the species distributions stated in the key below should be regarded as tentative.

As explained below, different preservation techniques will alter certain key morphological characters.

TERMINOLOGY AND MORPHOLOGY

The bryozoan colony is composed of numerous zooids, all physically and physiologically connected (Fig. 13.1). The feeding organ is a cluster of ciliated tentacles called a **lophophore**, which captures particles suspended in the water (Fig. 13.2). To accommodate many tentacles, the dorsal side of the lophophore is deflected inward to make a horseshoe shape (Fig. 13.3 A). In species with few tentacles, the lophophore is circular in outline (Fig. 13.3 B).

The outermost part of a zooid is a nonliving layer called an **ectocyst**, composed of either chitin or a slimy mucopolysaccharide. The ectocyst ranges from transparent to opaque, sometimes within the same species, depending on age, growth rate, and other factors. The inner part of the zooid is the **polypide**, which includes the lophophore and the entire digestive tract. The polypide can be shifted toward the zooid tip to extend the lophophore. When the zooid is alarmed, the entire polypide is quickly retracted and the lophophore becomes fully protected (Fig. 13.2).

Statoblasts are essentially tiny packages of yolky material and germinal cells enclosed within a bilayered case. The case is the "hard part" mentioned earlier, and it can be essential for species identification. There are several types of statoblasts: **floatoblasts** are freely released and have a peripheral ring of gas-filled chambers for buoyancy (Figs. 13.4 A and 13.5). **Sessoblasts** are firmly attached to the substratum (Figs. 13.4 B and 13.10). Zooids in the Fredericellidae produce reniform **piptoblasts** that generally remain with the substratum but are not firmly attached (Fig. 13.9).

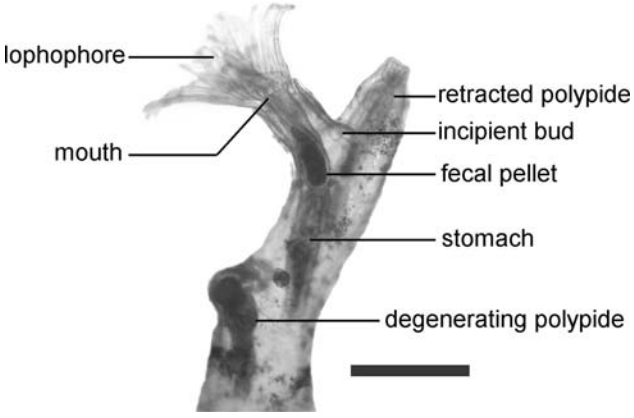


FIGURE 13.2 Zooids of a phylactolaemate bryozoan. Scale bar = 0.5 mm.

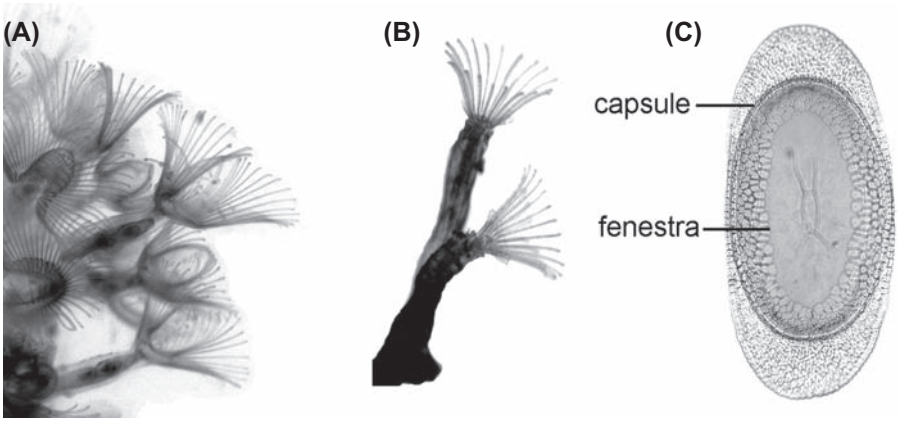


FIGURE 13.3 Aspects of bryozoan colonies. (A) Horseshoe-shaped lophophores typical of most phylactolaemate species; (B) circular lophophores of fredericellid species; (C) uninflated floatoblast of *Plumatella fruticosa* distinguishing the capsule from the fenestra. Scale bar = 0.5 mm.

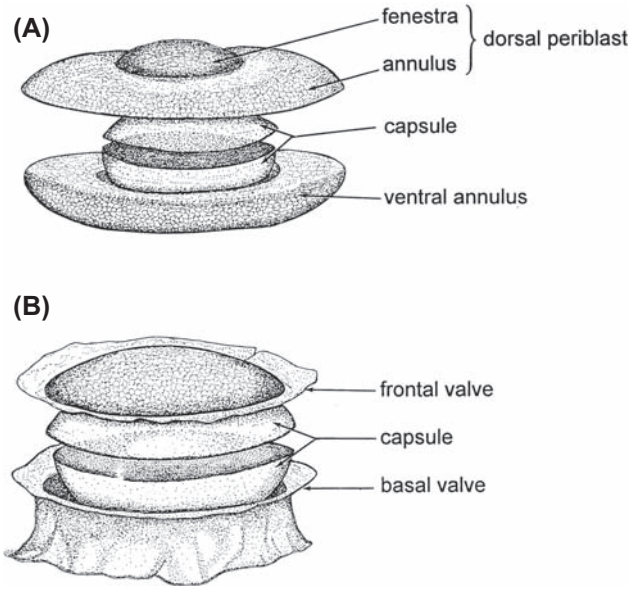


FIGURE 13.4 Sclerotized components of generalized phylactolaemate statoblasts in exploded view. (A) Floatoblast; (B) Sessoblast.

All statoblasts are formed like two halves of a clam shell that split apart at the time of germination. Each half, or valve, is normally composed of two layers: an inner capsule and an outer periblast (Fig 13.4). The capsule has no taxonomic value, but the **periblast** bears a wide variety of morphological features. In floatoblasts the periblast includes a ring of gas-filled chambers. In the center of this ring is an area called the **fenestra**. The relative dimensions of the periblast and its fenestra can be useful taxonomic features (Fig. 13.12). By convention, the valve with the smallest fenestra is considered dorsal and the opposite side is ventral (Figs. 13.5 and 13.12 A).

Several terms are useful in describing statoblasts. The line where the valves join together is called a **suture** (Fig. 13.7). **Tubercles** are pimple-like protuberances that may occur on various regions of the statoblast surface (Fig. 13.11 A). The reticulum is a net-like pattern of raised lines (Fig. 13.5). **Pitting** is the appearance of small depressions seen in certain fredericellid statoblasts (Fig. 13.9 A) Nodules are very small, rash-like dots visible only with SEM (Fig. 13.11 A). In addition, there are pores within the floatoblast annulus chambers that may have taxonomic significance (Fig. 13.11 C) (see Rubini et al., 2011). A more recently used structure is a **hypertubercle**, defined as a small tubercle atop a larger one (Fig. 13.11 B), a feature that defines the genus *Rumarcanella* (Hirose & Mawatari, 2011). Examining a floatoblast in side view (suture toward the viewer) can help determine whether or not the valves are laterally symmetrical (Fig. 13.6).

Statoblasts are never formed by freshwater ctenostome bryozoans. Instead, the dormant phase of the life cycle is represented by modified zooids called **hibernaculae**. Currently the hibernaculae of various species are too poorly known for them to be assigned any taxonomic value.

MATERIAL PREPARATION AND PRESERVATION

Standard procedure is to fix and preserve bryozoans in either 5% formalin or 70% ethyl alcohol. For molecular genetics, 100% ethyl alcohol is the preferred preservative. For histological work the best fixative is buffered glutaraldehyde, with the buffer concentration at 0.01M, not 0.1M as for many other invertebrates.

Many investigators like to preserve specimens with the lophophores extended, and for this the material must be narcotized. Menthol (crystals or molded wafers) is very effective and convenient, even though menthol has a low melting point and tends to melt under higher temperature field conditions (Wood, 2005b). The solid menthol is floated on the water surface in a small, closed container with the specimen. Exposure time varies with temperature and

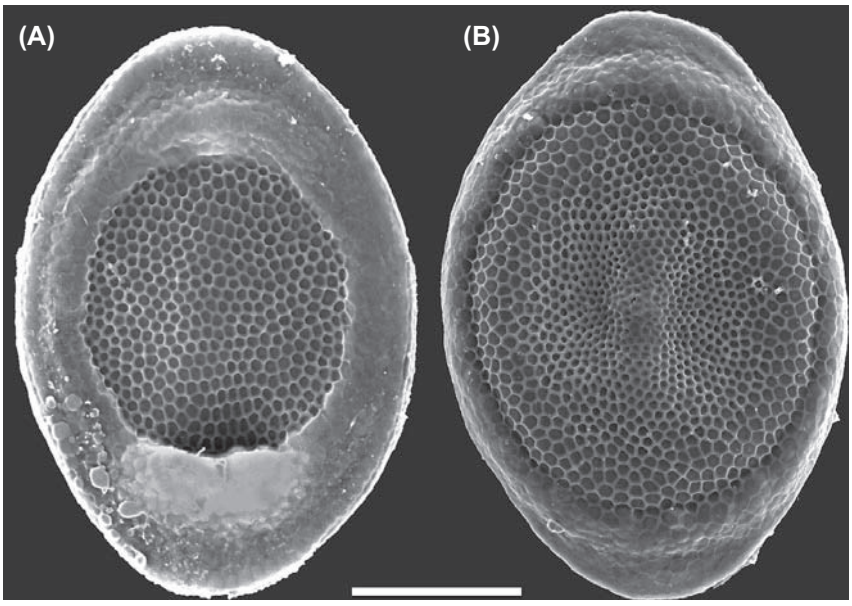


FIGURE 13.5 Floatoblast valves of *Plumatella vaihiriae.* (A) Dorsal valve; (B) Ventral valve. Scale bar = 100 μm.



FIGURE 13.6 Floatoblast lateral symmetry. (A) Typical asymmetry of *Plumatella fungosa*; (B) Typical symmetry of *Plumatella nitens*. Scale bar = 100 μm.

species, but seldom exceeds 1 h. The other alternative is to administer a chloral hydrate solution, drop by drop, and mix it over several hours. This is much less damaging to sensitive tissues than menthol, but chloral hydrate is difficult to obtain in countries that list it as a controlled substance.

For close examination the statoblast valves must often be separated and cleaned in a strong solution of potassium (or sodium) hydroxide. If you are in a hurry, heat the statoblasts in the solution in a spoon over a flame for no more than a minute. Then transfer the statoblasts to fresh water and tease apart the valves. The capsule valves may or may not separate from the periblast, depending on the species.

To view the frontal valve, it is best to separate and clean the valves in hot KOH or NaOH, then place them in clean fresh water and examine the frontal valve with substage illumination.

Statoblasts may be infrequent and difficult to find; if the ectocyst cannot be seen through, try using strong substage lighting; also check the surrounding substratum for brown to orange, reniform statoblasts left behind by a disintegrated part of the colony.

When examining statoblast valves, keep in mind that you can detect structures only on the fenestra, not on the annulus. Even then, you will not see faint reticulation or nodules. Tubercles and reticulation can be easily confused because under the light microscope they appear very similar. Usually tubercles act as tiny lenses, and as you focus up and down you can reduce them to little points of light. With most reticulation you can focus up and down and the pattern will just go in and out of focus without forming points of light. However, there are times when you really cannot tell the difference between tubercles and reticulation without scanning electron microscopy.

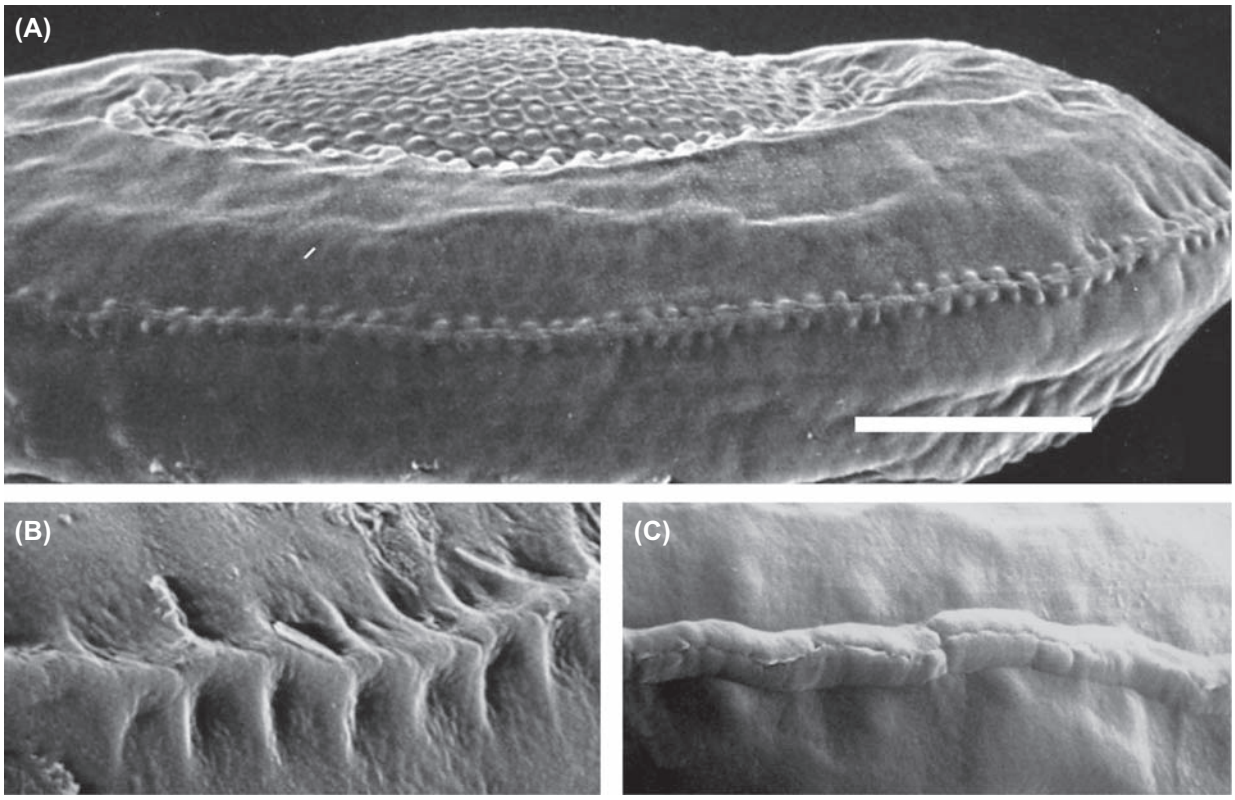


FIGURE 13.7 Floatoblast sutures. (A) *Plumatella repens,* scale bar = 50 μm; (B) *Plumatella fungosa*; (C) *Plumatella rugosa.*

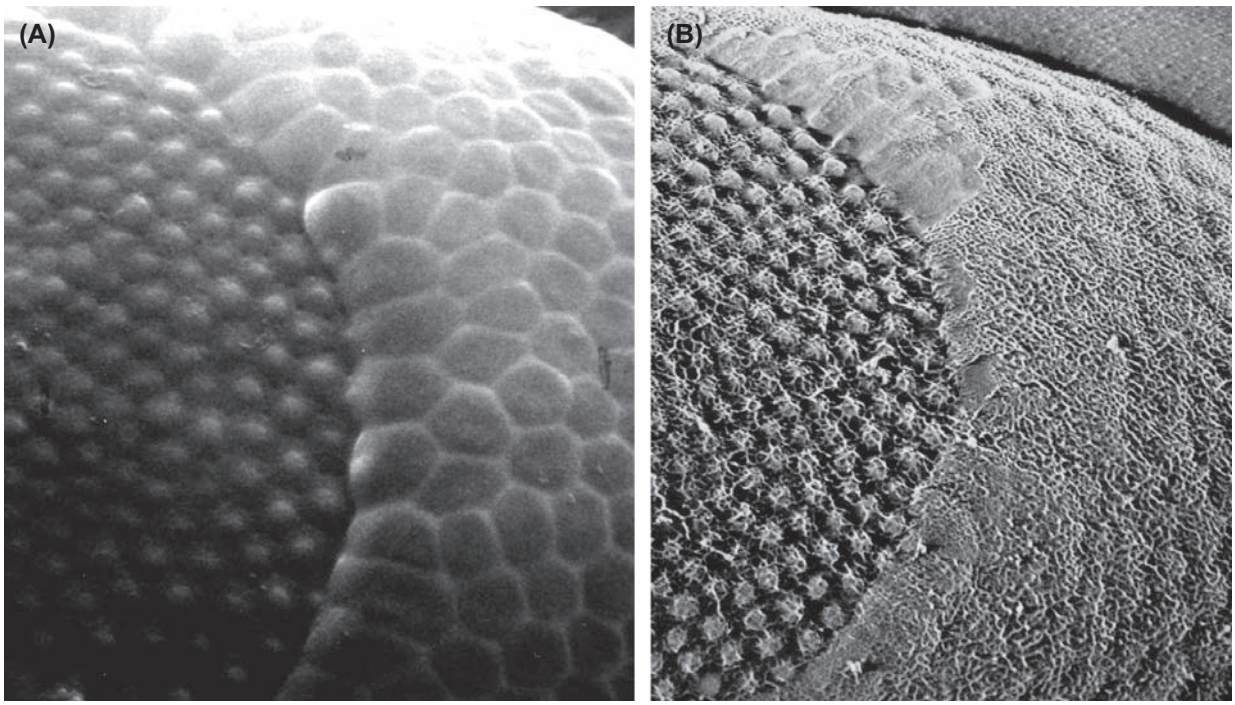


FIGURE 13.8 Floatoblast surface features. (A) *Plumatella emarginata* showing typical "paved" annulus; (B) *Plumatella mukai* showing typical wrinkled features. Scale bar = 50 μm.

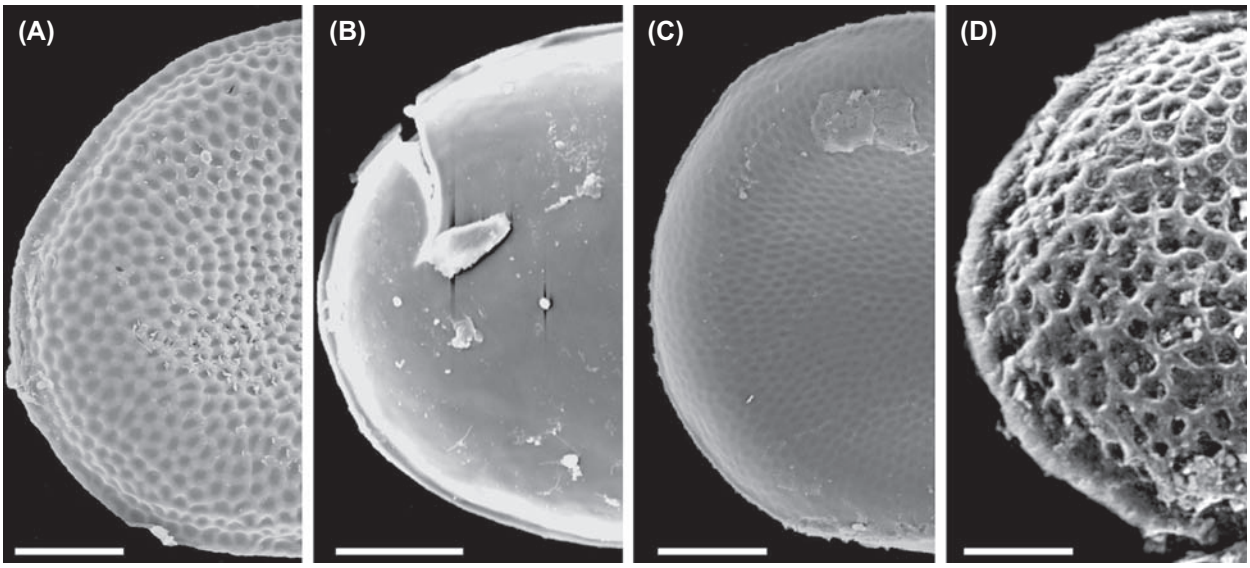


FIGURE 13.9 Four fredericellid species. (A) *Fredericella indica*; (B) *Fredericella sultana*; (C) *Fredericella toriumii*; (D) *Internectella bulgarica.* Scale bar = 50 µm. *Modified from Hirose & Mawatari (2011), used by permission from the Japanese Society of Systematic Zoology.*

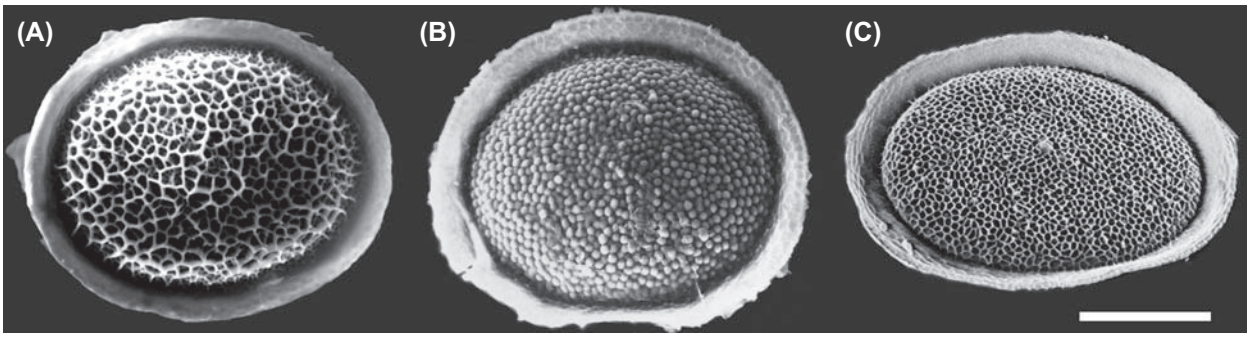


FIGURE 13.10 Sessoblast surface features. (A) Irregular reticulation of *Plumatella reticulate*; (B) Tubercles common in many species, in this instance, *Plumatella repens*; (C) Regular reticulation of *Plumatella vaihiriae*, which sometimes thickens to form pores. Scale bar = 100 µm.

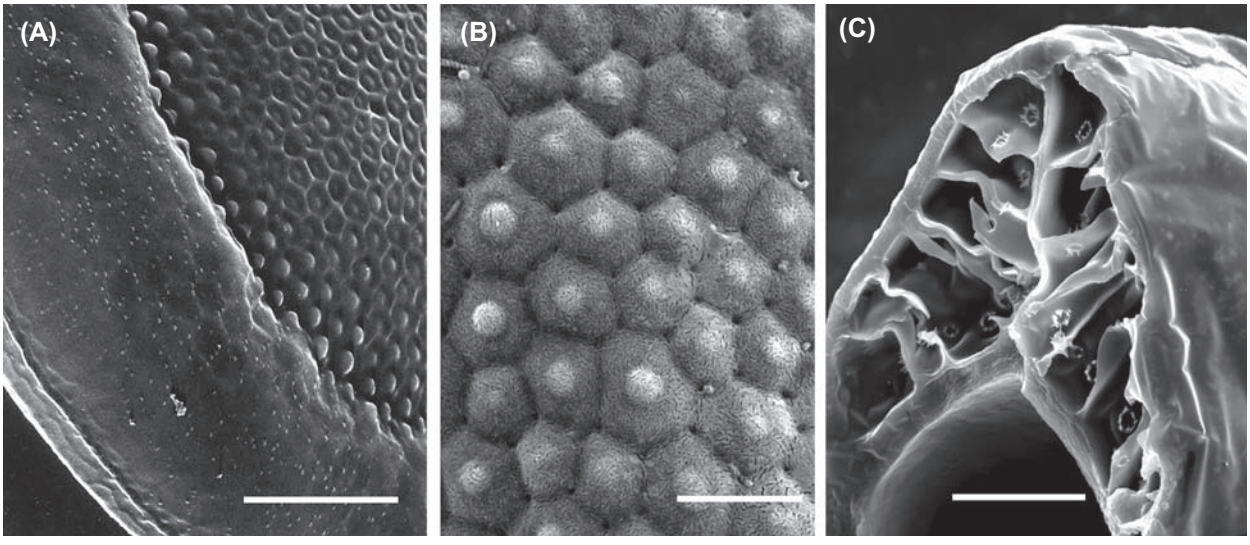


FIGURE 13.11 Floatoblast surface features. (A) Partial view of floatoblast in *Plumatella semilirepens* showing nodules on the annulus and both tubercles and reticulation on the fenestra. Scale bar = 25 µm; (B) Hypertubercles on floatoblast fenestra, characteristic of *Rumarcanella* species, in this instance *R. siamensis*. Scale bar = 10 µm; (C) A section of the floatoblast annulus showing chamber pores. Scale bar = 20 µm. *Photograph by M. Taticchi.*

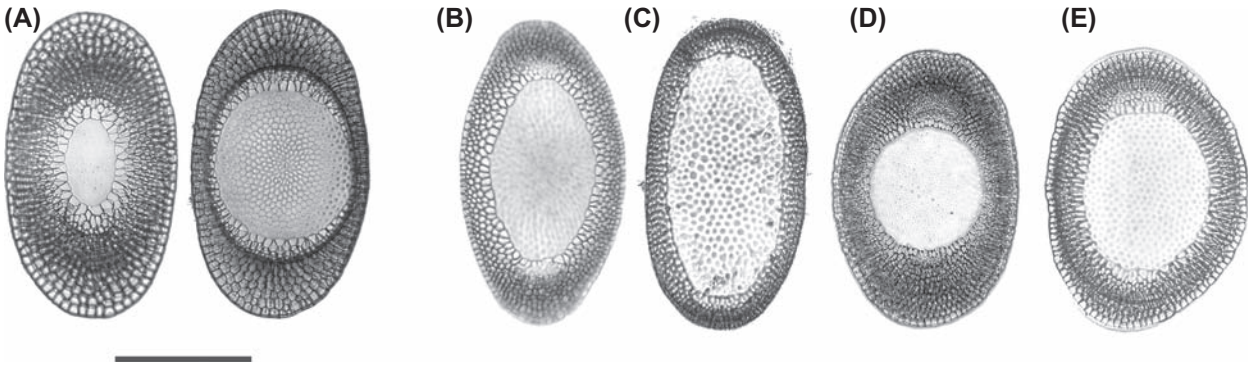


FIGURE 13.12 Isolated floatoblast valves all dorsal except as noted. (A) *Plumatella emarginata* (dorsal and ventral valves); (B) *Plumatella casmiana*; (C) *Plumatella repens*; (D) *Plumatella geimermassardi.* Scale bar = 100 µm.

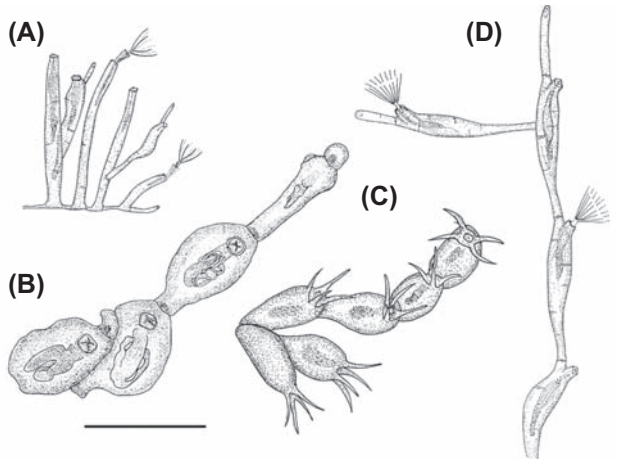


FIGURE 13.13 Ctenostome bryozoan colonies. (A) *Victorella pavida*; (B) *Hislopia prolixa*; (C) *Hislopia placoides*; (D) *Paludicella articulata*. Scale bar = 1 mm. *(B) From Hirose & Mawatari (2011), used by permission from the Japanese Society of Systematic Zoology; (C) modified from Abrikosov (1924).*

It is a common mistake to confuse the statoblast capsule with the fenestra. This can lead to errors in species identification. In fresh material, the amber-colored capsule is generally hidden by gas chambers of the annulus. But when the gas is lost in preserved specimens, the capsule is fully visible, and the outlines of the fenestra are less distinct (Fig. 13.3 C).

Statoblasts can be prepared for SEM by simply drying and sputtering on aluminum pins. Normally the ventral valve will collapse, which does not affect species identification. However, if you are finicky about such things you can always use critical point drying to retain the original shape. To check the statoblast surface texture, place a statoblast in the smallest possible drop of water on a microscope slide, push it out of the drop of water using a fine needle (it will dry quickly and shrivel slightly), then check the surface with reflected light to see whether it is dull or shiny.

Identifying bryozoan species often requires taking measurements of the statoblast using an optimal micrometer, and this brings up a sensitive subject. The literature is filled with incorrect measurements because statoblast valves being measured had been either dried or flattened under a coverslip when the data were taken. Simply separating the valves also can greatly alter their shape. Even placing a statoblast in alcohol can change its original dimensions. It is also true that under normal conditions statoblast sizes can vary considerably within a species and often within a single colony. Thus, whenever possible take measurements from fresh material in water, measure numerous statoblasts and calculate a statistical mean, never rely on dimensions from separated valves or from statoblasts prepared for SEM, and approach published statoblast measurements with some caution.

KEYS TO ECTOPROCTA (BRYOZOA)

Ectoprocta: Classes

1 Extended lophophore U-shaped in outline (Fig. 13.3 A) with the exception of Fredericellidae; lophophore with more than 20 tentacles; orifice is circular when lophophore is withdrawn; internal septa infrequent; statoblasts may be present ..... **Phylactolaemata [p. 526]**

1′ Extended lophophore always circular in outline with fewer than 20 tentacles (Fig. 13.3 B); orifice appears quadrangular when lophophore is withdrawn; statoblasts never present; individual zooids separated by internal septa, although this is not always evident ..... Gymnolaemata, one order: **Ctenostomata [p. 529]**

Ectoprocta: Phylactolaemata: Families

1 Colony composed of a linear, branching series of zooids (Fig. 13.1 B); branches sometimes fused; statoblasts (if present) with smooth margins; tentacles fewer than 65 2

1′ Colony globular and either lobed or entire in outline (Fig. 13.1 A); statoblasts with peripheral spines, hooks, or pointed extensions; tentacles more than 65 4

2(1) Extended lophophore U-shaped in outline (Fig. 13.3 A); statoblasts may be freely released from the colony or firmly cemented to substratum (Fig. 13.4); tentacles more than 25 3

2′ Extended lophophore circular in outline (Fig. 13.3 B); statoblasts (piptoblasts) neither buoyant nor firmly cemented to the substratum (Fig. 13.9), formed especially in branches attached to substratum, but possibly missing in some specimens; tentacles fewer than 25 ..... **Fredericellidae [p. 526]**

3(2) Colony composed of delicate, transparent tubes embedded in a soft, gelatinous matrix; floatoblast circular or nearly so with net-like reticulation covering the entire surface ..... Stephanellidae, one species: *Stephanella hina* Oka, 1908 [Japan, Korean peninsula, probably China]

3′ Colony and floatoblasts not as above ..... **Plumatellidae [p. 526]**

4(1) Mouth region without red pigmentation, lophophore lacking pair of white spots 5

4′ Mouth region with red pigmentation; prominent pair of white spots at end of each lophophore arm; statoblasts round with hooked spines radiating from the annulus perimeter; colony gelatinous and slimy, ranging from a flat sheet to a 0.25-m-long mass; common and widely distributed ..... Pectinatellidae, one species: *Pectinatella magnifica* Leidy, 1851 [China, Czech Republic, France, Germany, Japan, Korean peninsula]

5(4) Colony distinctly linear, often exceeding 2 cm; statoblasts round with wiry, hooked spines radiating from fenestra perimeter of both valves; occurring mainly in oligotrophic waters ..... Cristatellidae, one species; *Cristatella mucedo* Cuvier, 1798 [Palaearctic]

5′ Colony not distinctly linear; statoblasts otherwise ..... **Lophopodidae [p. 528]**

Fredericellidae: Genera and Species

1 Statoblast not as below 2

1′ Statoblast with a prominent keel across the frontal valve; entire statoblast enveloped in a layer of large cells that inflate with gas for buoyancy; two types of statoblasts, the most common being a typical piptoblast, and the second type is a highly unusual, irregularly shaped structure achieving buoyancy with an envelope of gas-filled cells ..... *Internectella bulgarica* Gruncharova, 1971 [Bulgaria]

2(1) Piptoblast surface appearing smooth and shiny when dry 3

2′ Piptoblast surface appearing dull, rough, or granular when dry 4

3(2) Cleaned frontal valve showing weak pitting when viewed with substage illumination (Fig. 13.9 C) ..... *Fredericella toriumii* Hirose & Mawatari, 2011 [Japan: Honshu]

3′ Cleaned frontal valve showing no markings at all. (Fig. 13.9 B) ..... *Fredericella sultana* Blumenbach, 1779 [Palaearctic]

4(2) Piptoblast surface uniformly pitted (Fig. 13.9 A); piptoblasts well separated ..... *Fredericella indica* Annandale, 1909 [Germany, Japan, Norway]

4′ Piptoblast surface bearing a rough, raised reticulum; piptoblasts often occurring in pairs. (Fig. 13.9 D) ..... *Internectella bulgarica* Gruncharova, 1971 [Europe: Bulgaria]

Ectoprocta: Phylactolaemata: Plumatellidae: Genera

Although Vinogradov's (2004) Hyalinellidae makes sense morphologically, it is not currently supported by genetic data and is, therefore, included in Plumatellidae.

1 Colony wall thick, soft, and hyaline; zooids forming low mounds when polypides are retracted; floatoblast length more than 450 µm. 2

1′ Floatoblast and colony not as above ..... ***Plumatella* and *Rumarcanella* [p. 527]**

2(1) Colony branches short and profuse, often fused, surrounded by thick, hard-gelatinous ectocyst; floatoblasts' surface covered with minute spines; a large, blunt process situated in the center of the ventral fenestra; a smaller process occurs in the center of the sessoblast frontal valve ..... *Gelatinella toanensis* Hôzawa & Toriumi, 1941 [China?, Japan, Korean peninsula]

2′ Colony branches long and sparsely branched, sometimes fused; floatoblast surface smooth, annulus not inflated prior to release; sessoblasts never formed ..... *Hyalinella punctata* Hancock, 1850
[Widely distributed]

Ectoprocta: Phylactolaemata: Plumatellidae: *Plumatella* and *Rumarcanella*: Species

1 Floatoblast length at least twice the length of dorsal fenestra (Figs. 13.12 A, D) 2

1′ Floatoblast length less than twice the length of dorsal fenestra (Figs. 13.12 B, C, E) 8

2(1) Colony and sessoblast not as below 3

2′ Colony with long, slender branches often free of the substratum; sessoblast length more than twice the width; often found in cool, oligotrophic waters ..... *Plumatella fruticosa* Allman, 1844
[Palaearctic]

3(2) Floatoblast distinctly asymmetrical in lateral view (Fig. 13.7 A); dorsal valve nearly flat, ventral valve deeply convex 4

3′ Floatoblast valves almost equally convex (Fig. 13.6 B); sessoblast surface roughened by a distinctive network of raised lines (Fig. 13.10 A); internal septa slightly oblique ..... *Plumatella reticulata* Wood, 1988
[Israel, Italy]

4(3) Floatoblast ventral valve reticulated, lacking tubercles (the distinction between tubercles and reticulation can often be difficult using light microscopy, however, in this case the reticulation is so prominent there should be little trouble) 5

4′ Floatoblast ventral valve tuberculated 6

5(4) Floatoblast length more than three times the length of dorsal fenestra; rare in the Palaearctic, documented from a power plant cooling lagoon in Bulgaria ..... *Plumatella bombayensis* Annandale, 1908
[Bulgaria. Oriental region]

5′ Floatoblast length less than three times the length of dorsal fenestra; floatoblast dorsal annulus bulging around inner capsule to form a distinct shoulder (Fig. 13.6 A) (several species will show a "capsule bulge" when the floatoblast is dry, but only this species has such a bulge when wet, and the feature is best seen on the dorsal side); sessoblast with reticulum or deep pits, but lacking tubercles (Fig. 13.10 C); uncommon but often locally abundant, especially in warm, eutrophic waters ..... *Plumatella vaihiriae* Hastings, 1929
[Italy, Spain, United Arab Emirates]

6(4) Colony not as below 7

6′ Colony forming tight masses of fused tubules without free branches, colonies capable of exceeding 1 cm thick ..... *Plumatella fungosa* Pallas, 1768
[British Isles, northern Europe, Russia]

7(6) Floatoblast surface smooth except for fenestra tubercles (sometimes absent on the dorsal fenestra) (Fig. 13.11 A); sessoblast surface uniformly tuberculated (Fig. 13.10 B); internal septa perpendicular to colony wall; common and widely distributed ..... *Plumatella emarginata* Allman, 1844
[Palaearctic]

7′ Floatoblast surface, including tubercles, appear wrinkled, a feature conspicuous with SEM and otherwise sometimes visible by reflected light (Fig. 13.8 B) (the wrinkled surface feature is best seen with scanning electron microscopy, however, it can sometimes be detected with a compound microscope using reflected (not transmitted) light) ..... *Plumatella mukaii* Wood, 2001
[China?, Japan]

8(1) Floatoblast fenestrae length less than 1.5 times the width (Figs. 13.13 D, E) 9

8′ Floatoblast fenestrae lengths more than 1.5 times the width (Figs. 13.12 B, C); tentacles fewer than 28 ..... *Plumatella casmiana* Oka, 1907
[Widely distributed]

9(8) Floatoblast dorsal annulus extending evenly from suture to fenestra without bulging around the inner capsule; sessoblast surface densely tuberculate 10

9′ Floatoblast dorsal annulus bulging around inner capsule to form a distinct shoulder (Fig. 13.5) (several species will show a "capsule bulge" when the floatoblast is dry, but only this species has such a bulge when wet, the feature is best seen on the dorsal side); entire floatoblast surface covered with raised reticulum (Fig. 13.5); sessoblast with reticulum or deep pits, but lacking tubercles Fig. 13.10 C); uncommon but often locally abundant, especially in warm, eutrophic waters ..... *Plumatella vaihiriae* Hastings, 1929
[Italy, Spain, United Arab Emirates]

10(9) Average floatoblast length less than 400 µm; colony not as below; the following couplets may require statoblast examination by SEM; if there is no access to SEM, you may refer to all species in couplets 11 through 19 as belonging to the "*Plumatella repens* group" 11

10′ Average floatoblast length greater than 400 µm; colony forming tight masses of fused tubules without free branches, colonies capable of exceeding 1 cm thick; floatoblasts laterally asymmetrical with the dorsal valve almost flat; SEM shows tuberculated floatoblast annulus ..... *Plumatella fungosa* Pallas, 1768
[Widely distributed]

11(10)	Floatoblast length-to-width ratio greater than 1.5	12
11′	Floatoblast length-to-width ratio less than 1.5	13
12(11)	Floatoblast laterally asymmetrical, the dorsal valve almost flat, the ventral valve deeply convex; SEM shows smooth annulus with nodules on the annulus ..... *Plumatella viganoi* Taticchi, 2010 [Italy: Umbria, Lake Trasimeno]	
12′	Floatoblast laterally symmetrical, both valves equally convex; SEM shows lumpy annulus with no nodules; fenestra with hypertubercles (Fig. 13.11 B) ..... *Rumarcanella vorstmani* Toriumi, 1952 [China?, Japan]	
13(11)	Ratio of floatoblast length to dorsal fenestra length greater than 2	14
13′	Ratio of floatoblast length to dorsal fenestra length less than 2	15
14(13)	SEM shows nodules and no reticulation of dorsal floatoblast valve ..... *Plumatella timwoodi* Taticchi, Elia, Todini, & Prearo, 2012 [Italy: Ternu, Lake Piediluco]	
14′	SEM shows reticulation but no nodules on dorsal floatoblast valve ..... *Plumatella trasimenica* Taticchi, Elia, Todini, & Prearo, 2012 [Italy: Umbria, Lake Trasimeno]	
15(13)	Average floatoblast length 350–400 µm	16
15′	Average floatoblast length less than 350 µ	17
16(15)	SEM shows floatoblast annulus smooth with nodules; floatoblast suture bordered on each side by a single row of large tubercles (Fig. 13.11 A) ..... *Plumatella repens* Linnaeus, 1758 [Widely distributed]	
16′	SEM shows floatoblast annulus roughed by concave outer cell walls; floatoblast suture is a simple cord (Fig. 13.8 B) ..... *Plumatella rugosa* Wood, Wood, Geimer, & Massard, 1998 [Widely distributed]	
17(15)	SEM shows no distinct reticulation on the floatoblast	18
17′	SEM shows distinct reticulation on the floatoblast; floatoblast suture lacking a border of large tubercles; annulus marked by rounded contours of underlying cell structure; nodules sparse ..... *Plumatella similirepens* Wood, 2001 [Italy]	
18(17)	Sessoblasts may be present; SEM shows floatoblasts bearing tubercles, but no hypertubercles; dorsal valve shown in Fig. 13.12 E ..... *Plumatella geimermassardi* Wood & Okamura, 2004 [British Isles, continental Europe]	
18′	Sessoblasts unknown (Toriumi (1955) claimed to have found sessoblasts, but there are no documenting specimens, and investigators has since been unable to confirm this observation—if sessoblasts do indeed occur they must be rare); SEM shows floatoblast fenestrae bearing hypertubercles (Fig. 13.12 B) ..... *Rumarcanella minuta* Toriumi, 1941 [Japan, Oriental region]	

Ectoprocta: Phylactolaemata: Lophopodidae: Genera and Species

1	Colony not distinctly compound	2
1′	Colony distinctly compound, composed of multiple clusters of zooids forming a large, loose, gelatinous mass; polypides capable of retracting completely without bending the digestive tract; statoblasts over 1 mm diameter, roughly discoid but bent across two axes..... *Asajirella gelatinosa* Oka, 1891 [China?, Japan, Korean peninsula]	
2(1)	Youngest zooids all around colony perimeter; oldest zooids near the center, colonies compact, less than 2 cm in any dimension	3
2′	Youngest and most numerous zooids all at one side of the colony, giving the colony a fan shape; colonies often joined by tough, mucus-like strings; statoblasts tapering to a point at each pole ..... *Lophopus crystallinus* Pallas, 1768 [Europe]	
3(2)	Polypides unable to withdraw completely without bending the gut; colony footprint seldom larger than 1 cm; statoblasts oblong and truncated, with 6–8 spines along the suture at opposite poles, each spine bearing a series of tiny hooks ..... *Lophopodella carteri* Hyatt, 1868 [Holarctic]	
3′	Polypides able to withdraw completely without bending the gut; colony footprint approaching 2 cm; colonies often forming a single compound structure (see Couplet 1); statoblasts over 1 mm diameter, roughly discoid but bent across two axes ..... *Asajirella gelatinosa* Oka, 1981 [China?, Japan, Korean peninsula]	

Ectoprocta: Gymnolaemata: Ctenostomata: Families

1 Tentacles numbering more than eight, zooids mostly recumbent, hibernaculae otherwise 2

1′ Tentacles numbering exactly eight. Erect portion of zooid 0.6−1.6 mm long and only slightly contractile (Fig. 13.13 A); hibernaculae with short, marginal, forked projections; occurring in both fresh and brackish water .... Victorellidae, one species: *Victorella pavida* Kent, 1870 [Europe, Russia]

2(1) Zooid length less than twice the width and flattened against substratum. Uncommon. ..... Hislopidae, one genus: ***Hislopa*** **[p. 529]**

2′ Zooid length more than twice the width, zooids more or less cylindrical, rambling colonies (Fig. 13.13 D), many free branches, often appearing as silvery threads ..... Paludicellidae, one species: *Paludicella articulata* Ehrenberg, 1831 [Widely distributed]

Ectoprocta: Gymnolaemata: Ctenostomata: Hislopidae: *Hislopa*: Species

1 Oral spines present (Fig. 13.13 C) ..... *Hislopia placoides* Korotnev, 1901 [Russia: Lake Baikal]

1′ Oral spines lacking (Fig. 13.13 B) ..... *Hislopia prolixa* Hirose & Mawatari, 2011 [Japan]

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Chapter 14

Phylum Entoprocta

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INTRODUCTION

Entoprocta is a small phylum of about 150 described species (Nielsen, 2012) known almost entirely from marine habitats, with several species occurring in estuarine areas. Only two species have been described from fresh water: *Loxosomatoides sirindhornae* Wood, 2005 in Thailand and *Urnatella gracilis* Leidy, 1847 first reported from southeastern United States and now distributed worldwide (Oda, 1982). At least one additional freshwater species is known from Thailand but not yet described.

In general, entoprocts are small, sessile, filter-feeding animals. The freshwater species grow as colonies of interconnected zooids. They are most commonly found in flowing or lightly turbulent water. A dense population of *Urnatella* can cover all available hard substrates in a felty layer (Emschermann, 1987).

For many years entoprocts were included in the phylum Bryozoa along with a larger group called Ectoprocta (see Chapter 13). Similarities between the groups include sessile colonies (although many marine species are solitary), a U-shaped gut, and the use of ciliated tentacles to gather food. Potentially more significant are the apparent similarities in larval development (see Nielsen, 2012). However, despite much debate, the relationship has never been conclusive, and the weight of new evidence now places the entoprocts in a wholly independent phylum (Waeschenbach et al., 2012).

The following discussion focuses on *Urnatella gracilis*, the best known and most widely distributed freshwater entoproct, and the only species occurring in the Palaearctic.

TERMINOLOGY AND MORPHOLOGY

Urnatella gracilis grows as a stalk of articulating segments capped by a bulbous head bearing ciliated tentacles. The stalk is often branched, with each segmented branch

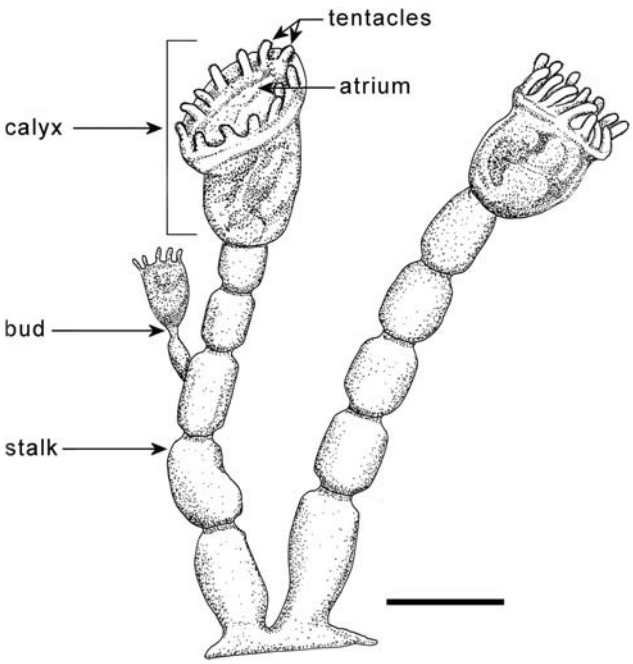


FIGURE 14.1 Entoproct colony of *Urnatella gracilis*. Scale bar = 1 mm.

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terminating in its own head, also called an **atrium** or **calyx** (Fig. 14.1). The stalk is almost entirely muscular except for a branching protonephridial system. The head includes all the organs and tissues required for the normal life functions of feeding, digestion, excretion, sexual reproduction, sensory perception, and nervous coordination. Tentacles bear several rows of cilia of varying sizes. The feeding current flows in a direction opposite from ectoproct bryozoans, drawn from near the base of the head and discharged away from the mouth. Particles trapped by cilia are thrown into a food groove along which they travel down the tentacle to the mouth opening.

Reproduction appears to be mostly asexual. Under certain optimal conditions the branching colonies of *Urnatella* develop special buds of 1-3 zooids that detach from the parent and drift away. These free buds may also creep slowly along the substrate by alternating contractions of longitudinal and transverse muscles (Emschermann, 1987). By this means the local population can grow very rapidly.

Sexual reproduction in *Urnatella* also has been described, but it appears to be a rare occurrence (Emschermann, 1965). Both ova and sperm have been observed in the same colony. It is believed that embryos are brooded one at a time and released as free-swimming larvae.

When environmental conditions become unfavorable, the head drops off and each of the stalk segments becomes a dormant hibernaculum with powers of regeneration. Overwintering occurs in this form. Resistance of the hibernaculum to desiccation and other environmental extremes has not been tested.

MATERIAL PREPARATION AND PRESERVATION

In the laboratory, dormant stalks of *Urnatella* colonies can remain viable in water for at least 3 years at 0–4°C. After germination at 15–20°C, they should be kept in circulating water and fed twice weekly from a culture of *Chlamydomonas* (Emschermann, 1987).

Entoproct colonies may be fixed and preserved in either 5% formalin or 70% ethyl alcohol. Attempts to narcotize with menthol are seldom very successful. For histological work, the best fixative is 2% glutaraldehyde solution in 0.01M sodium-cacodylate buffer at a pH of 7.4 for 1 h at around 23°C (Schwaha et al., 2010). Molecular genetics requires preservation in 100% ethyl alcohol.

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Chapter 15

Phylum Tardigrada

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INTRODUCTION

Tardigrades are xerophilous, hygrophilous, and hydrophilous micrometazoans categorized into two main classes (Eutardigrada and Heterotardigrada) with over 1200 species described from terrestrial, freshwater, and marine habitats. Commonly called "water bears," they must be surrounded by a film of water in order to be active. Cryptobiosis allows tardigrades to survive periods of desiccation in terrestrial habitats, but few freshwater and marine species are known to have this adaptation. Encystment occurs in some freshwater, moss dwelling, and soil tardigrades, possibly in response to stressful environmental conditions (e.g., oxygen depletion, pH alteration, and temperature variation). Some typically terrestrial species may inhabit freshwater environments, but most are probably "accidentals" washed into water during precipitation events (rainfall, flooding). Several taxa, however, are limnoterrestrial and colonize both terrestrial and freshwater habitats. The fewest number of taxa are obligate limnic species; however, the freshwater habitat has been investigated less frequently so it is difficult to estimate the total number of species. In the literature, the number of Palaearctic species in freshwater habitats is over 70, with about 30 species found exclusively or primarily in aquatic environments, although we expect the actual number to be much higher. These species are primarily eutardigrades that belong to two

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TABLE 15.1 Subdivision of the Phylum Tardigrada, With Habitat References (Guidetti & Bertolani, 2005; Marley et al., 2011; Bertolani et al., 2014)

I. Class Heterotardigrada
Order Arthrotardigrada (7 families, 44 genera, 176 species, marine, except *Styraconyx hallasi*, from Greenland springs close to the sea and also marine) Order Echiniscoidea Carphaniidae (1 species, freshwater, genus *Carphania*) Echiniscidae (14 genera, 249 species, mostly terrestrial, except for a few *Echiniscus*, *Hypechiniscus*, and *Pseudechiniscus*) Echiniscoididae (2 genera, 12 species, all marine) Oreellidae (1 genus *Oreella*, 3 species, terrestrial)
II. Class Mesotardigrada
Thermozodiidae (1 species, freshwater, genus *Thermozodium*; this class is considered dubious)
III. Class Eutardigrada
Order Apochela Milnesiidae (29 species, mostly terrestrial, 1 fossil species, 4 genera: *Milnesium* [rarely freshwater], *Limmenius, Bergtrollus*, and *Milnesioides*)
Order Parachela Necopinatidae (1 species, terrestrial, genus *Necopinatum*)
Super Macrobiotoidea Macrobiotidae (267 species, terrestrial and freshwater, 14 genera: Adorybiotus, Biserovus, Calcarobiotus, Famelobiotus, Insuetifurca, Macrobiotus, Minibiotus, Minilentus, Paramacrobiotus, Pseudohexapodibius, Richtersius, Schusterius, Tenuibiotus, Xerobiotus) Murrayidae (26 species, terrestrial and freshwater, 3 genera: Dactylobiotus, Macroversum, Murrayon)
Super Eohypsibioidea Eohypsibiidae (12 species, terrestrial and freshwater, 3 genera: *Austeruseus, Bertolanius, Eohypsibius*)
Super Hypsibioidea Hypsibiidae (161 species, terrestrial and freshwater, 14 genera: *Acutuncus, Adropion, Astatumen, Bindius, Borealibius, Diphascon, Hypsibius, Itaquascon, Mesocrista, Mixibius*[a], *Parascon, Pilatobius, Platicrista, Sarascon*) Microhypsibiidae (5 species, terrestrial and freshwater, 2 genera: *Fractonotus, Microhypsibius*) Calohypsibiidae (5 species, terrestrial, 1 genus: *Calohypsibius*) Ramazzottidae (36 species, terrestrial, 4 genera: *Hebesuncus, Ramazzottius, Ramajendas*°, *Thalerius*°)
Super Isohypsibioidea Isohypsibiidae (204 species, freshwater and terrestrial, rarely marine, 13 genera: *Apodibius, Dastychius, Doryphoribius, Eremobiotus, Halobiotus* (marine), *Haplohexapodibius, Haplomacrobiotus, Hexapodibius, Isohypsibius, Paradiphascon, Parhexapodibius, Pseudobiotus, Thulinius*) Beornidae (1 fossil species, [*Beorn leggi*])

[a]*The systematic position of the genus is debatable whether Isohypsibiidae or Hypsibiidae.* ° *The genus needs to be confirmed to belong here.*

orders and seven families (Table 15.1). This table updates a systematic list of the genera, families, and superfamilies found in Table 17.1 in Nelson et al. (2015) as a result of additional systematic revisions. The total numbers of species and records reported in the Palaearctic are much larger than in other zoogeographic realms, primarily due to the extensive effort of the early European tardigradologists, especially in Italy, Sweden, Germany, and France. We expect the global zoogeographic distribution of limnoterrestrial tardigrades, as previously reported in the literature, to undergo further analysis and revision as species groups and cryptic species are investigated more thoroughly (McInnes, 1994; McInnes & Pugh, 2007; Meyer 2013; Kaczmarek et al., 2014, 2015; Guidetti et al., 2015).

Hydrophilous tardigrades are benthic organisms that inhabit permanent freshwater habitats, crawling on aquatic

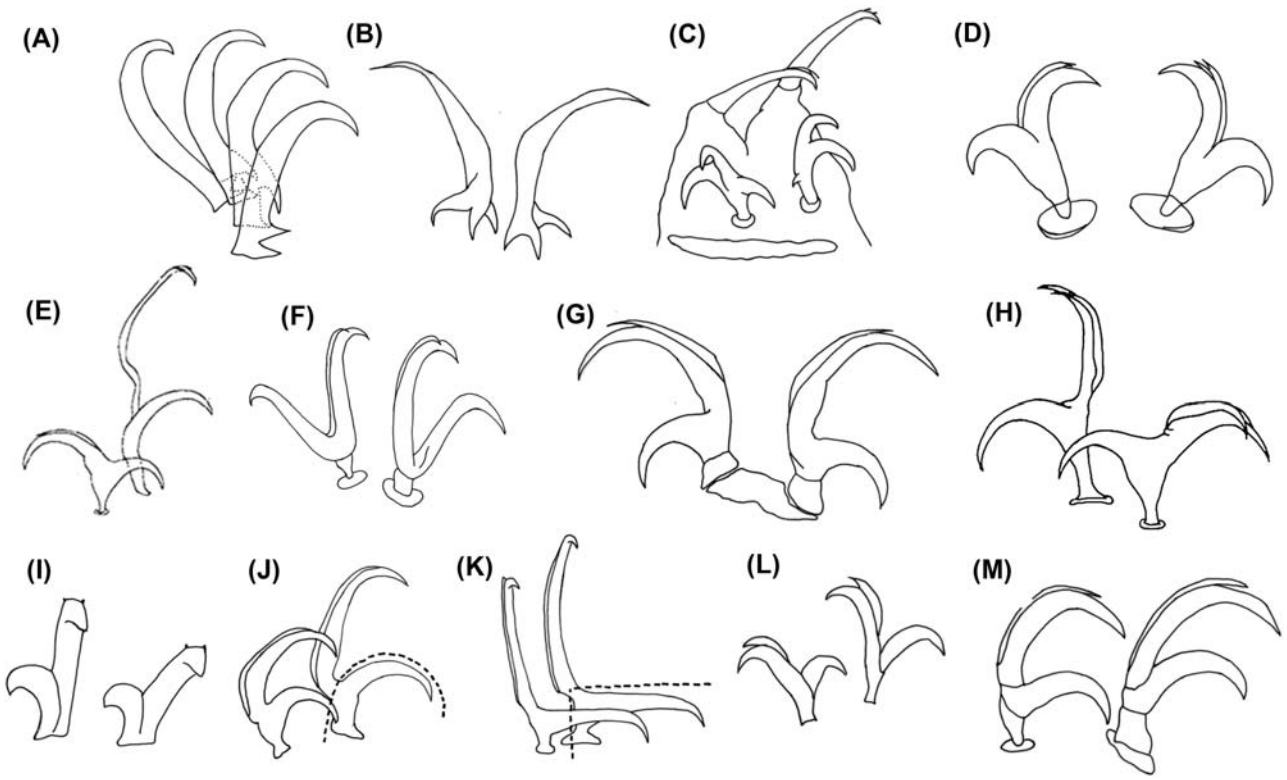


FIGURE 15.1 Diagrammatic representation of claw morphologies in tardigrades: (A and B) Heterotardigrada: (A) *Echiniscus*; (B) *Carphania*. (C–M) Eutardigrada: (C) *Milnesium*; (D) *Macrobiotus*; (E) *Ramajendas*; (F) *Murrayon*; (G) *Dactylobiotus*; (H) *Thulinius*; (I) *Calohypsibius*; (J) *Hypsibius*; (K) *Isohypsibius*; (L) *Microhypsibius*; (M) *Bertolanius*. *(A–D, F–K, and M) redrawn from Bertolani 1982; (E) redrawn from Pilato & Binda, 1990; (L) redrawn from Pilato, 1998.*

plants or in the interstitial spaces of sediments in lakes, rivers, streams, groundwater, and temporary or permanent ponds. They also live in subterranean caves, the hyporheic zone, activated sludge of sewage treatment plants, and cryoconite holes in glaciers.

LIMITATIONS

Tardigrade identification is based primarily on morphological variations in the claws, buccal-pharyngeal apparatus, cuticle, and egg shell. These characters are included in the key and shown in Figs. 15.1–14. We present a key to genera since many species are difficult to identify even by tardigrade taxonomists. Cryptic species are present, and many species groups need taxonomic revision. Although adult specimens are recommended for use in identification, juvenile eutardigrades are similar to adults. Sexual dimorphism in characters is known only for a few species. Revisions of genera, families, and superfamilies in recent years are based on a combination of molecular and morphological evidence (Sands et al., 2008; Guidetti et al., 2009; Jørgensen et al., 2010; Marley et al., 2011; Vicente et al., 2013; Bertolani et al., 2014).

TERMINOLOGY AND MORPHOLOGY

Tardigrades range in size from 50 μm in juveniles to over 1.5 mm. They have four pairs of legs usually with claws and a buccal-pharyngeal apparatus designed for piercing and sucking. The body is covered by a cuticle, which is molted periodically.

In echiniscid heterotardigrades (occasionally found in fresh water), each leg terminates in four unbranched claws in adults but only two claws per leg in the first instar. An unusual heterotardigrade, *Carphania*, is the only obligate freshwater genus; only one species is known from one record in a river in Sicily (Binda, 1978). *Carphania* has two claws on legs I–III and only one claw on reduced leg IV; all claws have two accessory points (as in eutardigrades) and four basal spurs (Fig. 15.1 B). *Carphania* is the only heterotardigrade with accessory points, thin cuticular structures that extend their distal portion free of the claw.

The limnoterrestrial eutardigrades usually possess two double claws on each leg, arranged as external and internal claws on the first three pairs of legs and as anterior and posterior claws on the hind legs. The claws on each leg may be similar or different in shape and size

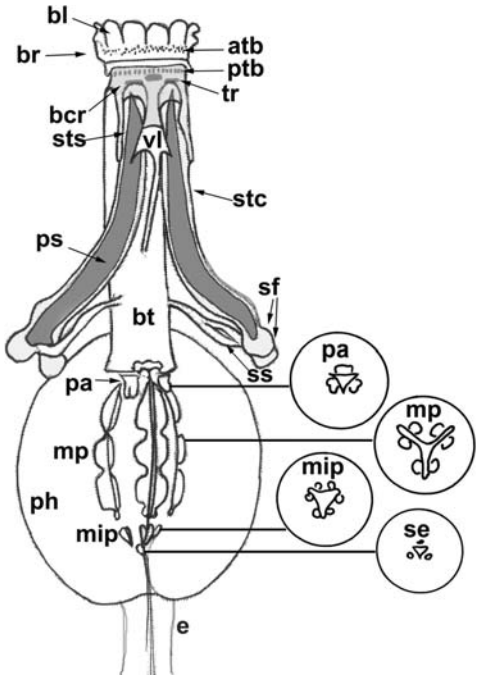


FIGURE 15.2 Diagrammatic representation of a tardigrade buccal-pharyngeal apparatus. NOTE: For this and subsequent figures in Chapter 15, the following abbreviations apply: *ap*, accessory points; *atb*, anterior band of teeth; *b*, basal portion; *bc*, buccal cirri; *bcr*, buccal crown; *bl*, peribuccal lamellae; *bp*, buccal papillae; *br*, buccal ring; *bt*, buccal tube; *c*, claws; *cA*, cirrus A; *cl*, clava; *co*, common tract; *ct*, cuticular plate; *e*, esophagus; *f*, filament; *l*, lunule; *lp*, lateral papillae; *mb*, main branch; *mip*, microplacoid; *mp*, macroplacoid; *op*, oral papillae; *pa*, pharyngeal apophyses; *ph*, pharynx; *pl*, placoids; *ptb*, posterior band of teeth; *ps*, piercing stylets; *s*, stylet; *sb*, secondary branch; *se*, septulum; *sf*, stylet furca; *sn*, spine; *ss*, stylet supports; *st*, stalk; *stc*, stylet coat; *sts*, stylet sheath; *tb*, teeth band; *tr*, transverse ridges; *vl*, ventral lamina. *Redrawn from Guidetti et al., 2012.*

(Figs. 15.1 C–M and 15.3). In true limnic species of eutardigrades, the claws are usually long or very long. Each double claw consists of a longer primary (main) branch with two accessory points, and a secondary branch without accessory points (Guidetti & Bertolani, 2005; Pilato & Binda, 2010).

In the eutardigrade order Apochela (Milnesiidae), there are no true double claws, since the two claw branches are separate from each other. The primary branch is long and thin and has accessory points, while the secondary branch is short, stout, and bears two or three hooks or spurs; the two claws of each leg are symmetrical (Fig. 15.1 C). In the eutardigrade order Parachela, the primary and secondary branches are connected and usually arise from a common basal tract, and the secondary branch has no hooks. However, in the limnic species *Isohypsibius deflexus* Mihelčič, 1960, the two branches of the external claws are not connected (Guidetti & Bertolani, 2005; Pilato & Binda, 2010). In many cases the base of the claw is surrounded by a cuticular lunule (Fig. 15.4). Cuticular bars, with taxonomic value at the species level, can be present on the legs in various positions.

Within the Parachela, the families Macrobiotidae and Murrayidae have symmetrical claws with a lateral-medial sequence of claw branches as follows: secondary branch of the external claw and its primary branch, primary branch of the internal claw and its secondary branch ("2-1–1-2 claws") (Figs. 15.1 D, F, G). Macrobiotidae have Y-shaped double claws (Figs. 15.1 D and 15.3 C), with the claw branches fused over a basal tract of variable length; Murrayidae have double claws with the two branches diverging immediately after the basal tract, V-shaped (Fig. 15.1 F) and L-shaped double claws (Figs. 15.1 G and 15.3 D). In the limnic *Dactylobiotus* (Figs. 15.1 G and 15.3 D) and *Macroversum* (Murrayidae), a cuticular link between the bases of the claw pair is present. The basal tract may consist of three parts: (1) a proximal stalk connecting the basal tract to the lunule; (2) a distal portion (which may be delimited by a transverse septum); and (3) a common tract after which the two claw branches diverge (Fig. 15.4) (Guidetti & Bertolani, 2005; Pilato & Binda, 2010).

All other families are characterized by asymmetrical claws ("2-1-2–1" claw sequence: secondary branch of the external claw and its primary branch, secondary branch of the internal claw and its primary branch) (Figs. 15.1 E, H–M). In Isohypsibiidae, the secondary branch is inserted perpendicularly (or at an obtuse angle) to the common basal tract of the claw. The external and internal claws are often similar in size and shape (*Isohypsibius*-type claw, Figs. 15.1 H, K and 15.3 B). In Hypsibiidae, the secondary branch of the external double claw forms a common arc with the basal tract; the external and internal claws are different in shape and size (*Hypsibius*-type claw, Figs. 15.1 E, J) (Guidetti & Bertolani, 2005; Pilato & Binda, 2010).

The buccal-pharyngeal apparatus is taxonomically important, especially in the eutardigrades. Basically, it consists of a mouth, buccal ring, buccal tube (totally or partially rigid) with protuberances for muscle attachments (e.g., buccal crown, dorsal and ventral apophyses), stylet mechanism, and a muscular sucking pharynx (usually containing bars or placoids) (Figs. 15.2 and 5–8). The presence and the number of cuticular structures around the mouth (peribuccal structures; Fig. 15.5) are significant at the generic level (Guidetti & Bertolani, 2005; Pilato & Binda, 2010; Guidetti et al., 2012, 2013).

The interior of the mouth may contain complex cuticular structures (buccal armature) consisting of anterior and posterior bands of small cuticular teeth (mucrones) followed by dorsal and ventral transverse ridges, which are species-specific characteristics (Figs. 15.2 and 15.5). Most eutardigrades have a completely rigid buccal tube, which is

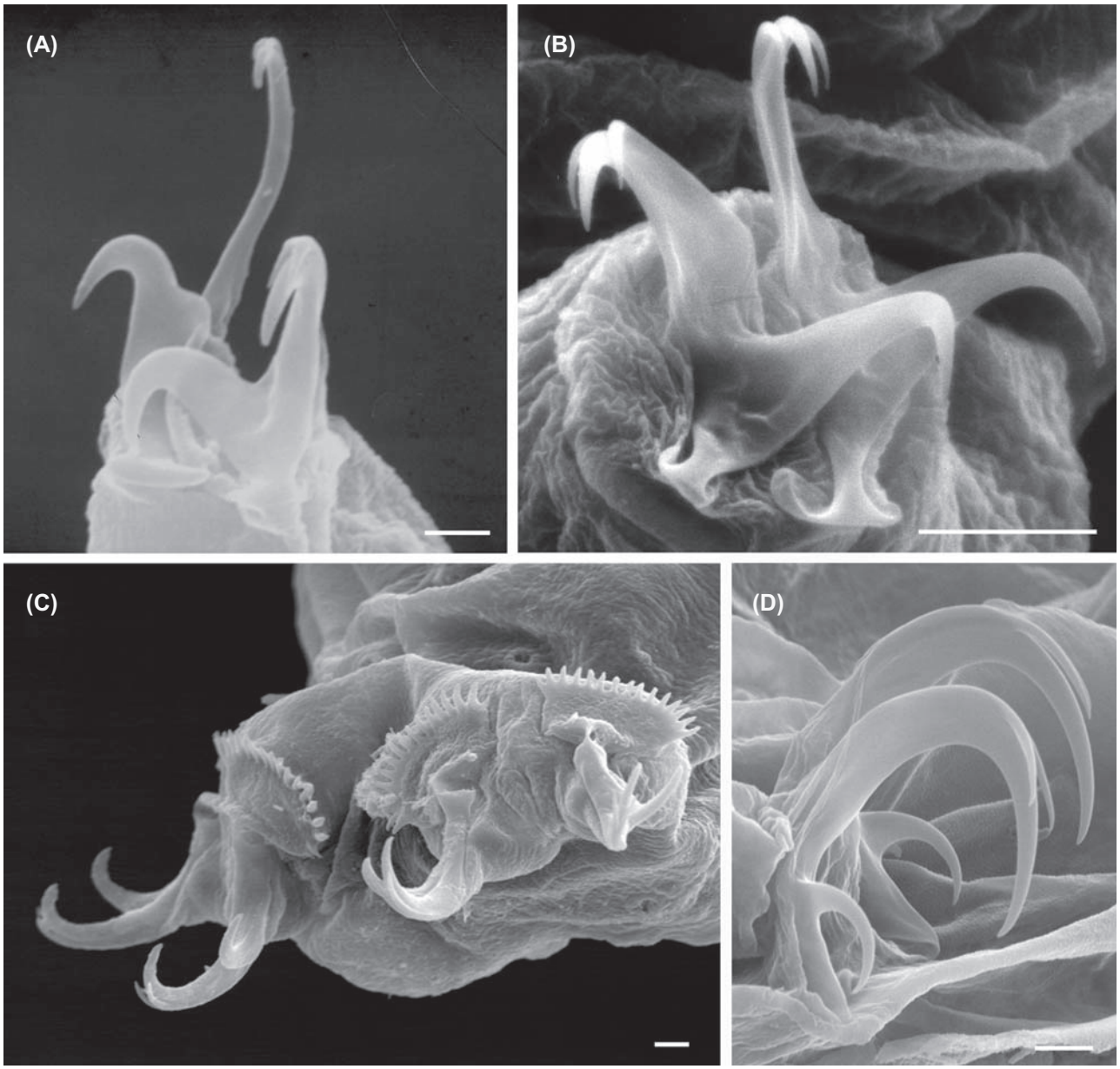


FIGURE 15.3 Scanning electron micrographs of eutardigrade claws: (A) *Ramazzottius oberhaeuseri*; (B) *Thulinius* sp.; (C) *Richtersius coronifer*; (D) *Dactylobiotus* sp. Scale bars = 5 μm.

supported by a ventral lamina (strengthening bar) (Figs. 15.2, 15.6 E–O, 15.7 A, and 15.8 A, B) in macrobiotids, murrayids, and several isohypsibiids (*Apodibius*, *Doryphoribius*, *Haplomacrobiotus*, *Haplohexapodibius*, *Hexapodibius*, *Parhexapodibius*). The murrayids *Dactylobiotus* and *Murrayon* have a deep hollow in the ventral lamina that in lateral view forms an evident hook (Fig. 15.8 A) (Guidetti & Bertolani, 2005; Pilato & Binda, 2010; Guidetti et al., 2012, 2013).

The wall of the anterior portion of the buccal tube is ventrolaterally surrounded by the buccal crown, which is composed of cuticular crests and laminae on which the stylet protractor muscles are attached (Figs. 15.2, 15.7, and 15.8) (Guidetti et al., 2012, 2013). In lateral view, the buccal crown shows apophyses that are taxonomically significant and vary in size and shape (e.g., crests as in *Isohypsibius*, *Thulinius*, and *Ramajendas*, hooks as in *Hypsibius*, lobes as in *Borealibius* and others; Fig. 15.8).

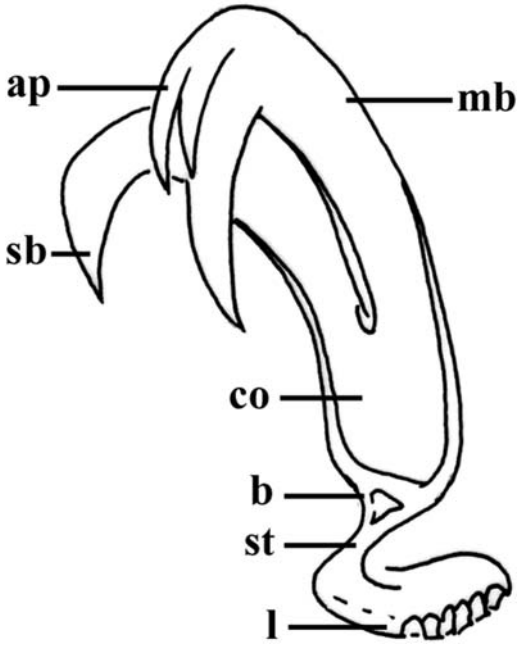


FIGURE 15.4 Diagrammatic representation of tardigrade claw structure. *Redrawn from Nelson & McInnes, 2002.*

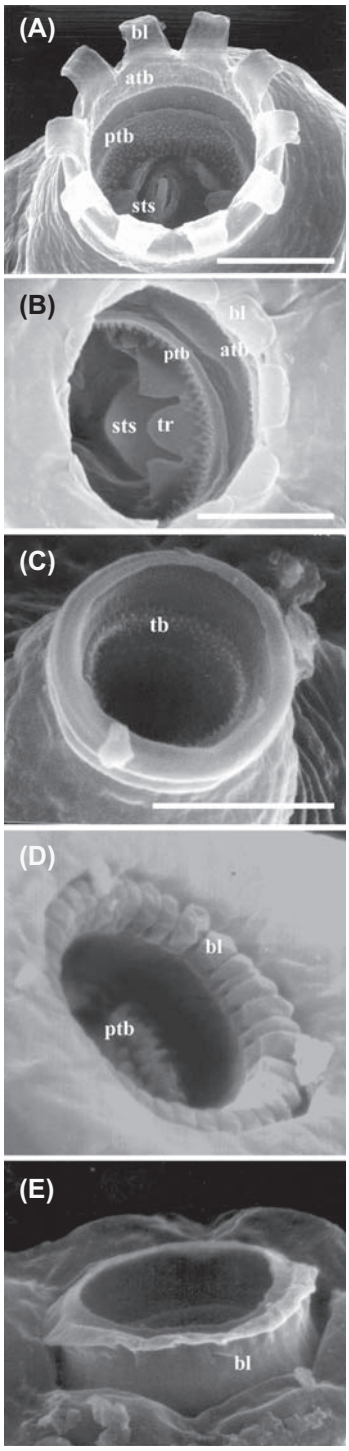


FIGURE 15.5 Scanning electron micrographs of eutardigrade mouth openings: (A) *Dactylobiotus selenicus*; (B) *Macrobiotus* sp.; (C) *Isohypsibius lunulatus*; (D) *Pseudobiotus* sp.; (E) *Thulinius* sp. Scale bars = 5 μm.

In some genera in different eutardigrade families (Milnesiidae, Hypsibiidae, Isohypsibiidae, Ramazzottiidae, Macrobiotidae, Eohypsibiidae) and in some echiniscid heterotardigrades, a rigid buccal tube between the buccal ring and the stylet supports is followed by a flexible, annulated pharyngeal tube from just below the stylet supports to the pharynx (Figs. 15.6 F, G, I–K and 15.7 C).

The buccal tube enters the tripartite pharynx, often terminating with three buccal tube apophyses functioning as valves. Lining the pharyngeal lumen are three cuticular bars in heterotardigrades (Figs. 15.6 A, B) including the limnic *Carphania fluviatilis* Binda, 1978 (Fig. 15.6 C) or three double rows of cuticular thickenings called placoids (Fig. 15.2), which are taxonomically significant in the Parachela (Eutardigrada). The placoids alternate in position with the three pharyngeal apophyses. The larger, anterior placoids (called macroplacoids) are in two or three transverse rows. Smaller, more posterior placoids (microplacoids) may be present and only in a single transverse row. In the same plane as each apophysis and posterior to the placoids, a single median thickening (septulum; three septula in a transverse row) may be present in some species. Microplacoids and/or septula can be present or absent and are taxonomically significant at the species level. In

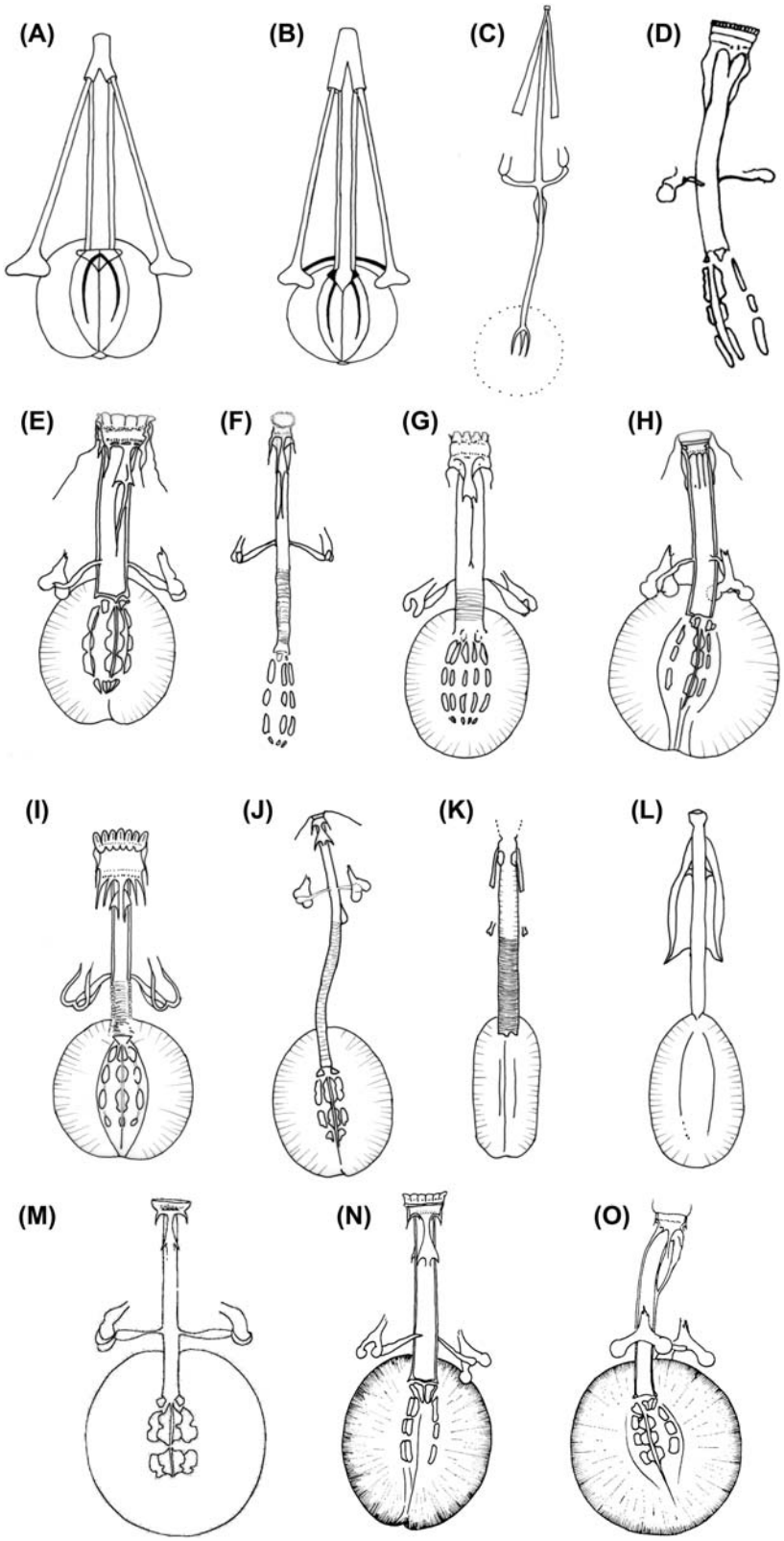


FIGURE 15.6 Diagrammatic representation of buccal-pharyngeal apparatuses: (A–C) Heterotardigrada: (A) *Echiniscus*; (B) *Pseudechiniscus*; (C) *Carphania*. (D–L) Eutardigrada: (D) *Pseudobiotus*; (E) *Macrobiotus*; (F) *Biserovus*; (G) *Insuetifurca*; (H) *Isohypsibius*; (I) *Eohypsibius*; (J) *Diphascon*; (K) *Astatumen*; (L) *Parascon*; (M) *Ramajendas*; (N) *Thulinius*; (O) *Doryphoribius*. *(A and B) redrawn from Kristensen, 1987; (C) redrawn from Binda & Kristensen, 1986; (D, E, H, J, K, N, and O) redrawn from Bertolani, 1982; (F and G) redrawn from Guidetti & Pilato, 2003; (I) redrawn from Bertolani & Kristensen, 1987; (L) redrawn from Pilato & Binda, 1987; (M) redrawn from Pilato & Binda, 1990.*

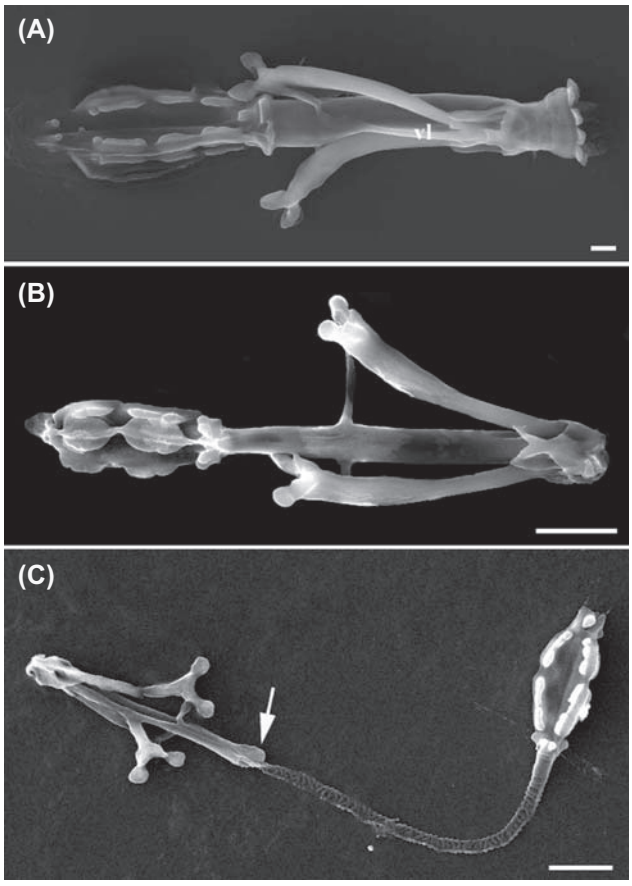


FIGURE 15.7 Scanning electron micrographs of eutardigrade buccal-pharyngeal apparatuses: (A) *Paramacrobiotus richtersi* with a ventral lamina on the buccal tube; (B) *Hypsibius dujardini* and (C) *Diphascon* sp. without a ventral lamina on the buccal tube. Arrow = drop-like thickening. Scale bars = 5 μm.

Apochela (e.g., *Milnesium*) and a few Parachela (e.g., *Itaquascon*, *Parascon*, *Astatumen*), the cuticular thickenings within the pharynx are reduced or absent (Fig. 15.6 L) (Guidetti & Bertolani, 2005; Pilato & Binda, 2010; Guidetti et al., 2012, 2013).

The cuticle and its processes are taxonomically important for identifying genera and species and often are different in the two extant classes of Tardigrada, Heterotardigrada and Eutardigrada (Nelson et al., 2015, Table 17.1). The classes are distinguished by the presence (in Heterotardigrada) or absence (in Eutardigrada) of a pair of cuticular cephalic cirri (called cirri A) (Figs. 15.9, 15.10 A, and 15.11 A). Heterotardigrada includes mainly the marine and armored terrestrial tardigrades, while its sister group, Eutardigrada, primarily encompasses unarmored freshwater and other terrestrial species.

Eggs are often essential for the identification of freshwater and terrestrial species (Fig. 15.12), especially in some eutardigrade genera in which the animals are morphologically very similar. Ornamented eggs are usually deposited freely and singly or in small groups. The ornamentation may include pores, reticulations, and processes with a wide variety of shapes, which have taxonomic significance. The laid eggs are often spherical or oval, with a diameter usually 50−100 μm but sometimes up to 235 μm, including the processes of the shell. Other eutardigrades and limnoterrestrial heterotardigrades (except *Carphania*, whose eggs are unknown, and *Oreella*, which has ornamented eggs laid freely) lay smooth eggs within the exuvium (Figs. 15.12 E, 15.13).

MATERIAL PREPARATION AND PRESERVATION

Collect limnic tardigrades and other freshwater interstitial meiofauna from sediments of lentic or weakly running lotic waters, floating vegetation, and periphyton via a core, dredge, grab, artificial substrate, or siphon. In lime and clay sediments, collect only the most superficial layer, but in sandy sediments tardigrades may live at greater depth. Stir the sand in a container of water and decant immediately after the sand settles. Filter the decanted water through a sieve (U.S. Standard No. 325) with pores of about 44 μm, and rinse the specimens from the screen into a Petri dish for examination or into sample jar for storage. A modified Boisseau apparatus can also be used for tardigrade extraction (Kinchin, 1994).

Alternatively, filter a watery suspension of the substrate through two stacked sieves with mesh openings of 500 μm or greater (top sieve) and 44 μm (bottom sieve). Examine the sediment remaining on the fine mesh sieve under a stereo-dissecting microscope, or centrifuge the sediment in water, sucrose, or Ludox at about 3000 rpm for 5 min. Pour the supernatant through the fine mesh sieve, and centrifuge the remaining sediment with a sucrose solution (density 1.18) at about 5000 rpm for 1 min. Ludox AM (DuPont product, colloidal silica, Sigma-Aldrich Chemical Co.) can be used in place of sucrose. Rinse the supernatant immediately through the fine mesh sieve thoroughly with running tap water, and wash the residue into a Petri dish for

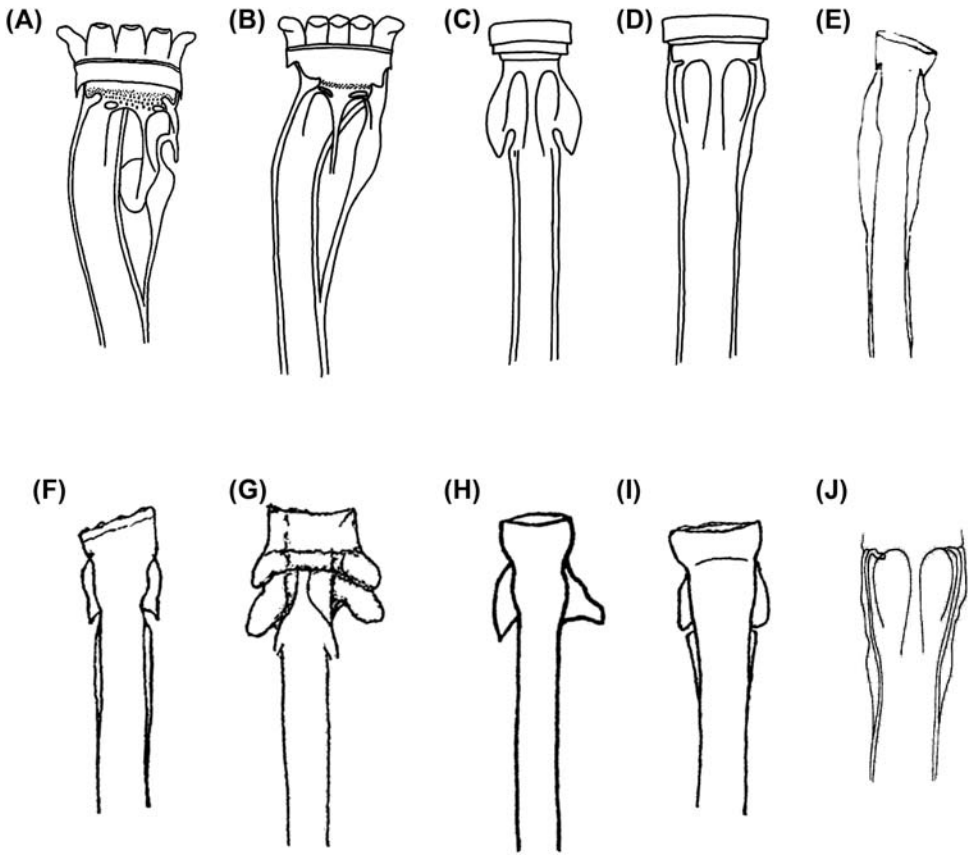


FIGURE 15.8 Diagrammatic representation of apophyses for the insertion of the stylet muscles on the wall of the buccal tube: (A) *Dactylobiotus*; (B) *Macrobiotus*; (C) *Hypsibius* and *Diphascon*; (D) *Isohypsibius*; (E) *Ramajendas*; (F) *Acutuncus*; (G) *Borealibius*; (H) *Bindius*; (I) *Mixibius*; (J) *Thulinius*. *(A–C) redrawn from Bertolani, 1982; (D) redrawn from Nelson et al. 1999; (E) redrawn from Pilato & Binda, 1990; (F–I) redrawn from Pilato & Binda, 2010; (J) redrawn from Bertolani, 1982.*

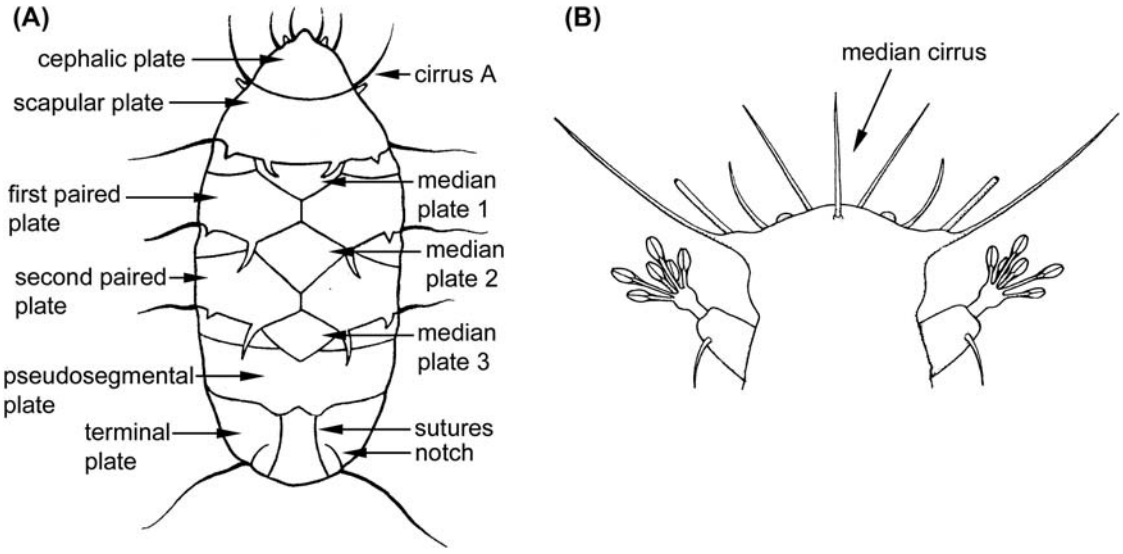


FIGURE 15.9 (A) Diagrammatic representation of dorsal cuticular plates of an echiniscoidid; (B) Diagrammatic representation of a head of an arthrotardigrade. *(A and B) redrawn from Ramazzotti & Maucci, 1983.*

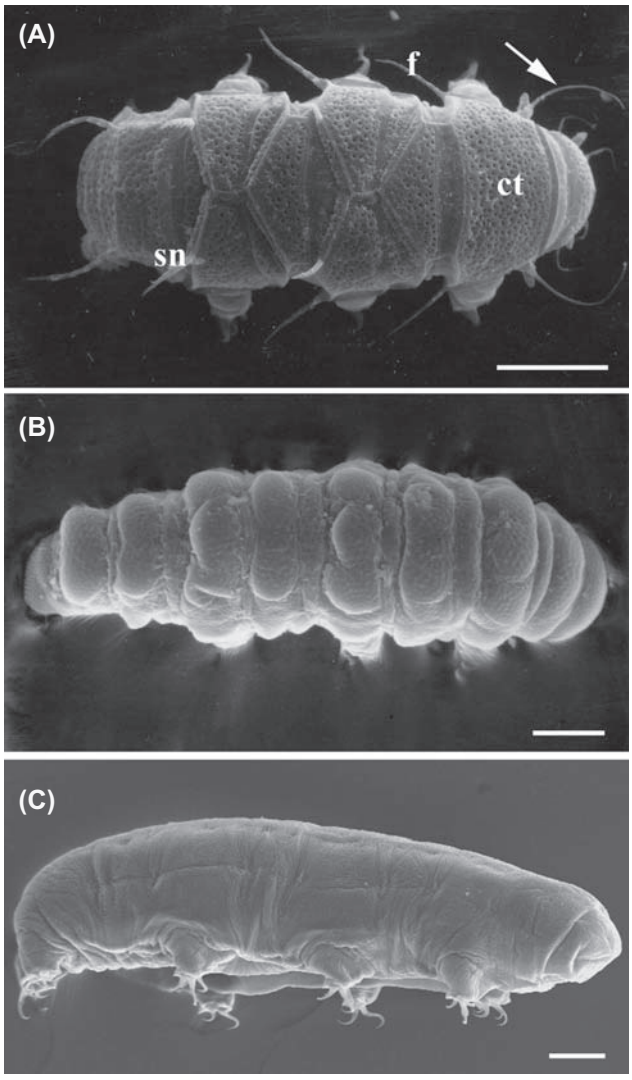


FIGURE 15.10 Scanning electron micrographs of tardigrades: (A) dorsal view of the heterotardigrade *Echiniscus duboisi* (arrow = cirrus A); (B) dorsal view of the eutardigrade *Isohypsibius lunulatus*; (C) lateral view of the limnic eutardigrade *Borealibius zetlandicus*. Scale bars = 25 μm.

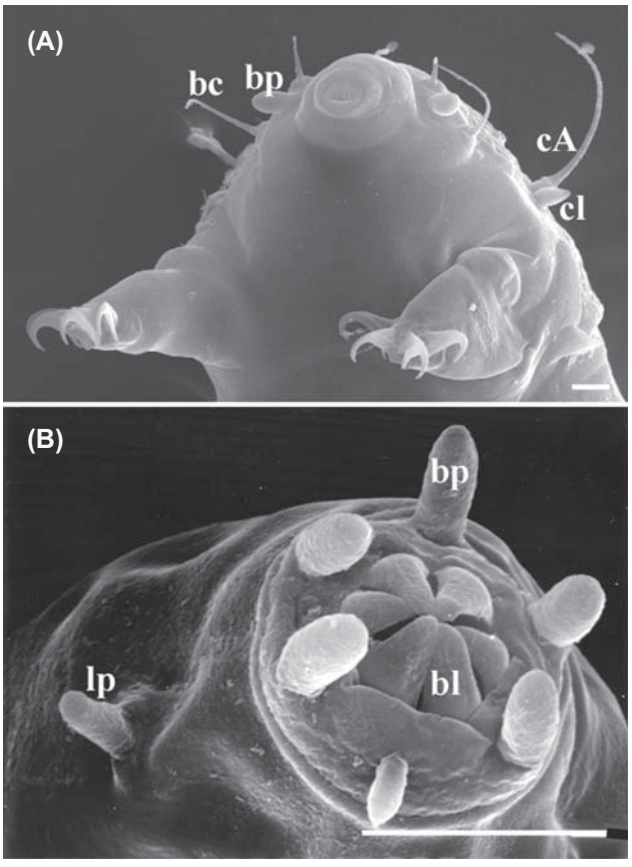


FIGURE 15.11 Scanning electron micrographs of tardigrade heads: (A) the echiniscid heterotardigrade *Antechiniscus parvisentus*; (B) the milnesiid eutardigrade *Milnesium cf. tardigradum From Bertolani et al., 2009*.

examination and preparation of microscope slides for identification.

If possible, mount individual specimens on microscope slides immediately and observe with phase contrast and/or differential interference contrast microscopy. Hoyer's mounting medium (50 mL distilled water, 30 g gum arabic, 150 g chloral hydrate, and 20 mL glycerol) produces cleared, distended specimens, but seal the coverslip (e.g., with epoxy paint) to ensure permanence. Reduce the amount of chloral hydrate to decrease the extent of clearing of specimens, and add 1 g potassium iodide (KI) to stain specimens slightly to increase the resolution of morphological structures. Since chloral hydrate is a controlled substance, other recommended media include Faure's medium, glycerin, polyvinyl alcohol, and polyvinyl lactophenol.

If not mounted on slides after extraction, preserve tardigrades in small amounts of water with Carnoy's fluid, boiling water, or boiling alcohol (85% or higher), but use alcohol to preserve specimens to be mounted later. Fixation shrinks the tardigrades, making them more difficult to identify. Moreover, specimens lose color in alcohol, and some characters (e.g., fine cuticular structures) are less visible. For molecular analysis (DNA extraction), preserve tardigrades in a very small amount of distilled water and freeze at −20°C, or preserve in ethanol.

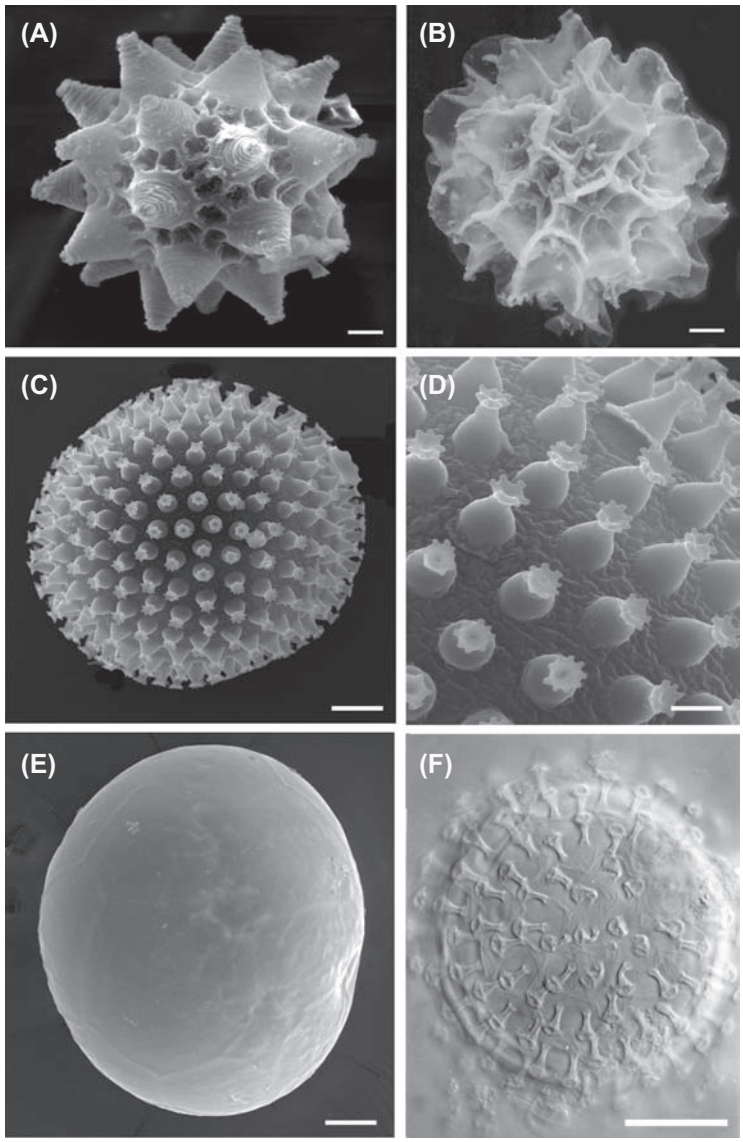


FIGURE 15.12 (A–D) Scanning electron micrographs of ornamented tardigrade eggs: (A) *Paramacrobiotus richtersi*; (B) *Bertolanius weglarskae*; (C) *Macrobiotus* gr. *hufelandi*; (D) magnification of C; (E) *Milnesium* cf. *tardigradum* smooth egg extracted from exuvium (F) light micrograph (differential interference contrast) of the ornamented egg of *Murrayon hastatus*. Scale bars (A–D), F = 25 µm, E = 8 µm. *(F) From Bertolani and Rebecchi, 1999.*

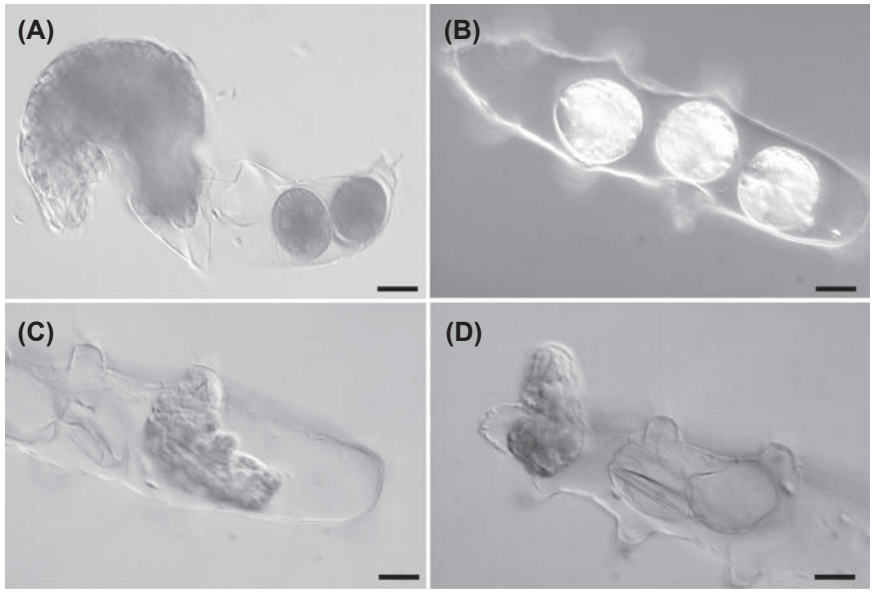


FIGURE 15.13 In vivo micrographs of *Diphascon* sp. (differential interference contrast). (A) animal releasing the eggs in the exuvium; (B) exuvium with three embryonate eggs; (C) newborn (juvenile) trying to find the exit from the exuvium; (D) newborn (juvenile) crawling out of exuvium. Scale bars = 50 µm.

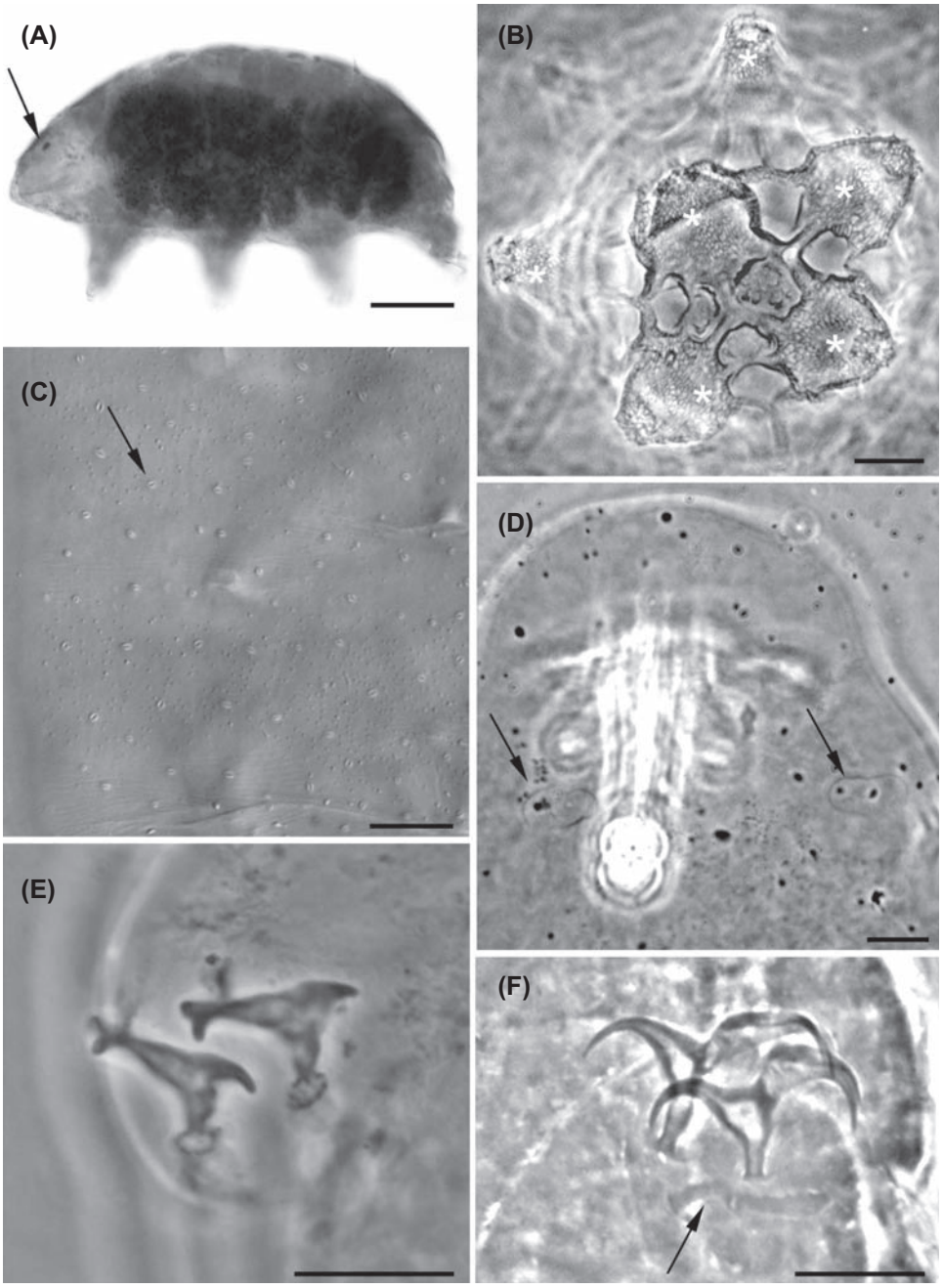


FIGURE 15.14 (A) *Echiniscus* sp. in vivo with an eyespot (*arrow*) (differential interference contrast). (B) Egg processes (asterisks) with reticulated walls of a *Paramacrobiotus* species (PhC). (C) Dorsal cuticle with pores of *Macrobiotus* species (arrow) (differential interference contrast). (D) Elliptical dorsolateral sense organs on the head of *Ramazzottius* (PhC). (E) Hind claws of *Eremobiotus* sp. (PhC). (F) Cuticular bars under the claw bases (*arrow*) of *Thulinius* (PhC). Scale bars: A = 100 μm, B–F = 10 μm.

KEYS TO TARDIGRADA

In the following keys we use "obligate" for genera with species that typically live in freshwater habitats, "limnoterrestrial" for genera with species that may be found in both freshwater and terrestrial habitats, and "accidental" for genera with species that typically do not live in freshwater habitats but may be rarely found or are accidently washed or blown into the aquatic habitat.

Tardigrada: Classes

1	Lateral cirri A present (Figs. 15.9, 15.10 A, and 15.11 A)	**Heterotardigrada**
1′	Lateral cirri A absent	**Eutardigrada**

Tardigrada: Heterotardigrada: Orders

1 Median cirrus usually present (Fig. 15.9 B); digits or claws directly inserted on the leg ..... Arthrotardigrada, one species: *Styraconyx hallasi* Kristensen, 1977 [Marine, but also found in Greenland springs]

1′ Median cirrus absent; each claw on a papilla inserted on the leg ..... **Echiniscoidea**

Tardigrada: Heterotardigrada: Echiniscoidea: Families

1 Four claws per leg in adults, cirrus A short to very long; with dorsal-lateral plates (Figs. 15.1 A, 15.9 A, and 15.10 A) ..... **Echiniscidae**

1′ Two claws on legs I–III, one claw on leg IV in adults; cuticle without dorsal plates; cirrus A very short; obligate ..... Carphaniidae, one genus: *Carphania*

Tardigrada: Heterotardigrada: Echiniscoidea: Echiniscidae: Genera

1 Pseudosegmental plate absent; median plates not subdivided; black or red eyespots (Fig. 15.14 A) 2

1′ Pseudosegmental plate present between second paired plate and terminal plate (Fig. 15.9 A); black eyespots; accidental ..... *Pseudechiniscus*

2(1) Terminal plate notched (Fig. 15.9 A); red eyespots; accidental ..... *Echiniscus*

2′ Terminal plate divided by sutures (Fig. 15.9 A); black eyespots (Fig. 15.14 A); accidental ..... *Hypechiniscus*

Tardigrada: Eutardigrada: Orders

1 Head without cephalic papillae; usually two double claws per leg (Figs. 15.1 D–M) ..... **Parachela**

1 Head with cephalic papillae, including two lateral papillae (Fig. 15.11 B); claws with the secondary branch not connected to the primary branch (Fig. 15.1 C); limnoterrestrial ..... Apochela, one genus: *Milnesium*

Tardigrada: Eutardigrada: Parachela: Superfamilies

1 Two double claws on each leg "asymmetrical," with sequence 2-1-2–1 (Figs. 15.1 E, H–M and 15.3 A); smooth eggs laid within the exuvium (Fig. 15.13) or ornamented eggs laid freely (Fig. 15.12) 2

1′ Two double claws on each leg similar in size and shape and "symmetrical," with sequence 2-1-1–2 (Figs. 15.1 D, F, G and 15.3 C, D); ventral lamina present (Figs. 15.2, 15.7 A, and 15.8 A, B); ornamented eggs laid freely (Fig. 15.12) ..... **Macrobiotoidea**

2(1) Internal and external claws of similar size and shape (Figs. 15.1 H, K–M and 15.3 B) 3

2′ Internal and external claws of clearly dissimilar size and shape (Figs. 15.1 E, J and 15.3 A); most with external claws of *Hypsibius* type, with secondary branch forming a common arc with the basal portion; most with smooth eggs laid within the exuvium ..... **Hypsibioidea**

3(2) Each double claw with three distinct but connected parts (*Eohypsibius*-type claw; Fig. 15.1 M); the internal claw can rotate and simulate a symmetrical arrangement with the external claw on the same leg; 14 peribuccal lamellae; eggs laid freely and ornamented ..... Eohypsibioidea, one family: **Eohypsibiidae**

3′ Claws with primary and secondary branch continuous with the basal portion; secondary branch of each claw forming a right angle (or wider) with claw base (Figs. 15.1 H, K); peribuccal lamellae present or absent; eggs laid within the exuvium ..... Isohypsibioidea, one family: **Isohypsibiidae**

Tardigrada: Eutardigrada: Parachela: Macrobiotoidea: Families

1 L or V shaped claws, i.e., with the two claw branches diverging immediately after the basal portion (Figs. 15.1 F, G); evident hook on the ventral lamina (Fig. 15.8 A) ..... **Murrayidae**

1′ Y-shaped claws, i.e., with claw branches fused over a tract of variable length (common tract) (Fig. 15.1 D); no evident hook on the ventral lamina ..... **Macrobiotidae**

Tardigrada: Eutardigrada: Parachela: Macrobiotoidea: Murrayidae: Genera

1 Very well-developed L-shaped claws, with cuticular thickenings connecting the base of the claws on each hind leg (Figs. 15.1 G and 15.3 F); with or without lunules 2
1′ V-shaped claws, with lunules (Fig. 15.1 F); limnoterrestrial ..... *Murrayon*
2(1) With lunules around the claw bases; obligate ..... *Macroversum*
2′ Without lunules; obligate ..... *Dactylobiotus*

Tardigrada: Eutardigrada: Parachela: Macrobiotoidea: Macrobiotidae: Genera

1 Cuticle without pores, three rod-shaped macroplacoids; microplacoid, if present, distant from the third macroplacoid more than its length (Fig. 15.7 A); eggs always with large reticulated processes (Fig. 15.14 B); limnoterrestrial ..... *Paramacrobiotus*
1′ Cuticle with (Fig. 15.14 C) or without pores; 2 or 3 macroplacoids; microplacoid, if present, close to the third macroplacoid; eggs with processes of various types; limnoterrestrial ..... *Macrobiotus*

Tardigrada: Eutardigrada: Parachela: Hypsibioidea: Families

1 Medium-sized or large claws 2
1′ Very small claws, with a narrow common portion continuous with the primary branch, on which the secondary branch is rigidly connected (Fig. 15.1 L); buccal tube narrow, three macroplacoids; limnoterrestrial..... Microhypsibiidae, one genus *Microhypsibius*
2(1) External claws of *Hypsibius* type (with secondary branch forming a common arc with the basal portion (Fig. 15.1 J) or simulating *Isohypsibius* type (with secondary branch forming a right angle with the basal portion; Figs. 15.1 H, K); most with smooth eggs laid within the exuvium; limnoterrestrial ..... **Hypsibiidae**
2'. Claws of *Ramazzottius* type, with primary branch of external claw very long and narrow, with very thin flexible connection to upper basal portion; basal portion of the external claw long and straight (Fig. 15.3 A); buccal tube rigid; elliptical dorsolateral sense organs on head (Fig. 15.14 D); ornamented eggs laid freely; accidental ..... Ramazzottiidae, one genus *Ramazzottius*

Tardigrada: Eutardigrada: Parachela: Hypsibioidea: Hypsibiidae: Genera

1 Buccal tube rigid, without posterior part of flexible and spiral composition; placoids in the pharyngeal bulb..... 2
1′ Buccal tube with posterior part of flexible and spiral composition (pharyngeal tube) (Figs. 15.6 J, K and 15.7 C); placoids in the pharyngeal bulb present, thin or absent 3
2(1) Apophyses for the insertion of the muscles of the stylets on the anterior part of the buccal tube hook shaped (Fig. 15.8 C); limnoterrestrial ..... *Hypsibius*
2′ Apophyses for the insertion of the muscles of the stylets on the anterior part of the buccal tube almost cylindrical in shape with a large rounded or bilobed projection (Fig. 15.8 G); limnoterrestrial ..... *Borealibius*
3(1′) More than one row of macroplacoids present in the pharyngeal bulb; annulation of the pharyngeal tube clearly visible at maximum magnification 4
3′ Macroplacoids absent, or present as a single thin and long strand; very fine annulation of the pharyngeal tube 8
4(3) Pharyngeal tube very thin and longer that the buccal (rigid) tube..... 5
4′ Pharyngeal tube shorter or as long as the buccal (rigid) tube; furcae of the stylets with posterolateral processes spoon-like; limnoterrestrial ..... *Platicrista*
5(4) Apophyses for the insertion of the muscles of the stylets on the anterior part of the buccal tube in the shape of "semilunar hooks" (Fig. 15.8 C) 6
5′ Apophyses for the insertion of the muscles of the stylets asymmetrical; the dorsal is triangular with rectilinear dorsal margin and posterior apex very distant from buccal tube, the ventral with arched margin and posterior apex nearer to buccal tube (Fig. 15.8 H); limnoterrestrial ..... *Bindius*
6(5) Drop-like thickening between the rigid and flexible (pharyngeal) portions of the buccal tube present..... 7
6′ Drop-like thickening between the rigid and flexible (pharyngeal) portions of the buccal tube absent; limnoterrestrial ..... *Adropion*
7(6) Two macroplacoids similar in length and in rows that look as parentheses, and with septulum in the pharynx; limnoterrestrial .... *Pilatobius*

7′ Three macroplacoids in a straight line, sometimes with microplacoid and/or septulum in the pharynx; limnoterrestrial ..... *Diphascon*

8(3) Stylet supports very thin, but present; limnoterrestrial ..... *Itaquascon*

8′ Stylet supports completely absent; only the most anterior part of the buccal tube is not annulated (Fig. 15.6 K); limnoterrestrial ..... *Astatumen*

Tardigrada: Eutardigrada: Parachela: Eohypsibioidea: Eohypsibiidae: Genera

1 Buccal tube rigid, without spiral composition 2

1′ Posterior part of buccal tube flexible, of very fine spiral composition (pharyngeal tube) (Fig. 15.6 I); limnoterrestrial ..... *Eohypsibius*

2(1) Large trumpet-shaped mouth; crest-shaped buccal tube apophyses for insertion of muscles of the stylets with a single pair of caudal hooks; limnoterrestrial ..... *Bertolanius*

2′ Tubular mouth; 2 to 6 hook-shaped appendages for insertion of the stylet muscles; limnoterrestrial ..... *Austeruseus*

Tardigrada: Eutardigrada: Parachela: Eohypsibioidea: Isohypsibiidae: Genera

1 Secondary branch of each claw forming right (or wider) angle with base; *Isohypsibius*-type claws (Figs. 15.1 H, K) 2

1′ Claws with very wide angle (about 180°) between the primary and the secondary branch at least on the internal claw on leg IV (Fig. 15.14 E); limnoterrestrial ..... *Eremobiotus*

2(1) Ventral lamina absent 3

2′ Ventral lamina present (Fig. 15.6 O); limnoterrestrial ..... *Doryphoribius*

3 Apophyses for the insertion of the muscles of the stylets on the anterior part of the buccal tube crest shaped and symmetrical (Figs. 15.8 D, L 4

3′ Apophyses for the insertion of the muscles of the stylets on the anterior part of the buccal tube hook shaped and asymmetrical (Fig. 15.8 I); limnoterrestrial ..... *Mixibius*
[Systematic position is debatable whether Isohypsibiidae or Hypsibiidae]

4(3) Peribuccal lamellae around the mouth opening present (caution, may be difficult to see) (Figs. 15.5 A, B, D, E); very long claws (Fig. 15.1 H) 5

4′ Peribuccal lamellae around the mouth opening absent (Fig. 15.5 C); limnoterrestrial ..... *Isohypsibius*

5(4) About 30 peribuccal lamellae (Fig. 15.5 D); placoid row in a straight line; obligate ..... *Pseudobiotus*

5′ Twelve peribuccal lamellae present, often fused (Fig. 15.5 E) and then difficult to recognize with light microscopy; placoid row in the shape of a Grecian urn (Fig. 15.6 N); 1 or 2 cuticular bars under (but not connected to) the claw bases on legs I–III (Fig. 15.14 F); limnoterrestrial *Thulinius*

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Part II

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Chapter 16

Phylum Arthropoda: Introduction and Arachnida

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Introduction to Arthropoda

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INTRODUCTION

The phylum Arthropoda constitutes the largest and most morphologically diverse group of animals. Specific relationships among the taxa of this clade are only partially understood, as are the relationships between the Arthropoda and other possibly related phyla. One hypothesis unites the Arthropoda and the Annelida as the "Articulata" (reviewed in Scholtz, 2002), uniting the two groups based upon segmentation. More recently, the Arthropoda and the Nemata have been united in a larger group as the "Ecdysozoa," being all animals that molt (Aguinaldo et al., 1997).

Aquatic arthropods include the Chelicerata (mites and spiders), Myriapoda (aquatic millipedes), and the Crustacea (crustaceans, apterygotans, and insects). The Chelicerata are discussed herein, while Crustacea are described in Chapters 17–22.

The Diplopoda are the most diverse group within subphylum Myriopoda, and aquatic forms are exceedingly rare and localized (Geoffry, 2015). Most forms encountered in fresh water have fallen in, or live in, very moist terrestrial habitats associated with freshwater systems (for example, the hydrophilous species of *Typhloiulus* in southern European caves (Antić et al., 2017). However, one cave species from northern Italy is at least semiaquatic.

TERMINOLOGY AND MORPHOLOGY

Arthropods all bear segmented bodies with segmented limbs. The Chelicerata body is divided into a cephalothorax, which contains the head, limbs, and thoracic organs, and an abdomen. The segmentation may be obscured due to body segments fusing, as in the mites. Chelicerates lack

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antennae, although the oral palpi may be elongated and serve a similar sensory function.

The Myriapoda have elongated bodies with serially homologous body segments, each bearing two pairs of limbs. In reality, each segment only has one limb pair, but the body "segments" are actually each two segments fused into one. Only one pair of antennae is present.

The Crustacea have the body divided into three divisions: head, thorax, and abdomen. The thorax typically may have three to seven pairs of ambulatory limbs, however, in the Branchiopoda there may be up to 19 pairs. The abdomen may have limbs as well, called pleopods or "swimmerettes," which can be used to propel the animal. Crustacea *sensu stricto* generally have two pairs of antennae, and the Hexapoda have one pair.

KEYS TO ARTHROPODA

Arthropoda: Subphyla

1	Less than 20 paired limbs; never more than 10 pairs for walking 2
1′	More than 10 pairs of identical walking limbs; millipedes..... ..... Myriopoda: Diplopoda, one species: *Serradium semiaquaticum* Enghoff et al., 1997
2(1)	Animal body variously separated into two divisions, cephalothorax and abdomen in spiders, and gnathosoma and idiosoma in mites; antennae absent; four pairs of legs (except larval mites, which have three); never with a bivalved carapace that can close entirely around the animal..... Chelicerata, one class: **Arachnida [p. 552]**
2′	Animal body divided into three or more divisions, and if fused, then body completely enclosed in a bivalved carapace; 1–2 pairs of antennae present ..... **Crustacea** (Chapter 17)

Arachnida: Subclasses

Arachnids are a large group of mainly terrestrial organisms classified in 15 extant orders (see Proctor et al., 2015). Representatives of four of these orders, Araneae (true spiders) and three orders of the subclass Acari (mites)—Mesostigmata, Sarcoptiformes, and Trombidiformes—are the only chelicerates habitually found in and around freshwater habitats. Among these, members of only a few groups of Sarcoptiformes and Trombidiformes are truly aquatic. Phylogenetic relationships of arachnid orders are not clearly understood, and the classification is undergoing substantial revision based on interpretation of morphological, behavioral, and genetic data. Here we follow the classification outlined by Proctor et al. (2015) in Volume I of this series.

1	Body conspicuously divided into cephalothorax and abdomen, spinnerets present, spiders ..... **Araneae [p. 552]**
1′	Body less conspicuously divided into gnathosoma (capitulum) and idiosoma, spinnerets absent, mites..... **Acari [p. 553]**

Arachnida: Aranae: Families

Aquatic spiders are poorly known. Only one truly submergent spider has been recorded; the Diving Bell Spider, *Argyroneta aquatica*. Certain members of the family Lycosidae and the genus *Dolomedes* (Pisauridae) are well known to actively hunt on the surface of lentic or slow lotic systems.

1	Eight eyes in two rows 2
1′	Eight eyes; upper eye row of four eyes with lateral-most eyes set posterior to middle eyes, such that it appears that there are three rows of eyes ..... Lycosidae [Cosmopolitan]
2(1)	Hunting on water surface, never diving; not building webs for prey capture ..... Pisauridae, one genus: *Dolomedes* [Cosmopolitan]
2′	Hunting underwater, from submerged air-filled web; captures prey in underwater web; adults collect air at surface and bring it underwater to fill retreats and nests .....Cybaeidae, one species: *Argyroneta aquatica* Clerck, 1757 [Palaearctic]

Arachnida: Acari: Orders and Suborders[1]

1 Three pairs of legs; genital field not developed; pedipalp genu with two setae *or* idiosoma bearing series of paired glandularia; larval and nymphal mites 2

1′ Four pairs of legs, pedipalp genu with one setae; idiosoma lacking series of paired glandularia; fully developed genital field with a functional gonopore present 3

2(1) Chelicerae typically chelate and dentate; pedipalps simple; prodorsum usually with a pair of well-defined bothridia bearing distinctively modified bothridial setae; opisthosoma usually bearing paired lateral glands ..... Order Sarcoptiformes, suborder Oribatida

2′ Chelicerae with fixed digit regressed and movable digit a hook or stylet-like structure; palps simple or with distal segments variously modified prodorsum lacking well-defined bothridia and with sensillae setiform; opisthosoma lacking paired lateral glands ..... Order Trombidiformes, Suborder Prostigmata
[Only Halacaridae is treated here.]

3(1) Chelicerae typically chelate and dentate; pedipalps simple; subcapitulum usually bearing rutellae or pseudorutellae; prodorsum usually with a pair of well-defined bothridia bearing distinctively modified bothridial setae; opisthosoma usually bearing paired lateral glands ..... Order Sarcoptiformes, suborder Oribatida

3′ Chelicerae with fixed digit regressed and movable digit a hook or stylet-like structure; palps simple or with distal segments variously modified; subcapitulum lacking rutellae; prodorsum lacking well-defined bothridia and with sensillae setiform; opisthosoma lacking paired lateral glands ..... Order Trombidiformes, Suborder **Prostigmata**
[Only Halacaridae is treated here.]

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[1]Note from D. C. Rogers: Despite several years of trying and requests to 22 specialists, we were unable to locate any author willing to treat Palaearctic mites as a whole. However, we are eternally grateful to Dr. Ilse Bartsch for her production of keys to the Halacaridae.

Arachnida: Acari: Trombidiformes: Halacaridae

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INTRODUCTION

The Halacaridae, superfamily Halacaroidea, includes exclusively benthic organisms. Halacarids are primarily marine; but in addition to more than 1000 marine species, there are 50–60 species that occur exclusively, mainly or at least regularly, in fresh water (Bartsch, 2009).

Four subfamilies (Astacopsiphaginae, Limnohalacarinae, Porolohmannellinae, and Ropohalacarinae (Viets, 1933; Bartsch, 1989, 2006) include exclusively freshwater genera, but with growing knowledge of the meiofauna, brackish water or even marine species or genera may be found that have to be assigned to one of these subfamilies. A few species are congeneric with marine taxa. Species of marine genera are included if they are found in brackish water or regularly in fresh or low-saline brackish water habitats.

TERMINOLOGY AND MORPHOLOGY

Most Palaearctic freshwater halacarids are 150 to 600 μm in length. The adult body is divided into an **idiosoma**, with the four leg pairs I to IV, and a **gnathosoma**, with **palps** and **chelicerae** (Fig. 16.1). The idiosoma is oblong, slightly or distinctly flattened. It is typically covered with sclerotized plates; the dorsal plates are an anterior and a posterior plate and a pair of **ocular plates** (Fig. 16.1); the latter may be reduced or absent. In general, the ornamentation of the plates is rather uniform, reticulate, foveate, or almost lacking. The basic number of idiosomatic setae and gland pores on the dorsum is six and five pairs, respectively. The number of both the setae and gland pores may be reduced; rarely a larger number of setae is found. The dorsal as well as ventral plates may be divided, reduced or enlarged, and fused to a dorsal or ventral shield.

The ventral plates consist of an anterior **epimeral plate** (by fusion of **epimera** I and II), a pair of posterior epimeral plates (by fusion of epimera III and IV), and a **genital or genitoanal plate** (by fusion of the genital and anal plate). The genital plate of adults includes the genital opening (Fig. 16.3). Females and males are similar in dorsal aspect but differ in the genital area. Females often have a larger genital opening, a lower number of setae around the genital opening, and an ovipositor which is visible through the genital plate. Males have an elaborate spermatopositor.

The gnathosoma consists of the gnathosomal base, rostrum, palps, and chelicerae. There are two pairs of maxillary setae; either one pair inserts on the gnathosomal base and one on the rostrum or both pairs on the rostrum. The palps have four articles, attached either lateral or dorsal to the gnathosomal base; the first and third articles are short, the second long (Fig. 16.2). The chelicerae are elongate and end with a claw; in some genera the chelicerae are styliform.

Adult halacarids have four pairs of legs. Legs I and II are directed forward, legs III and IV backward. The six segments of the legs of adults are **trochanter**, **basifemur**, **telofemur**, **genu**, **tibia**, and **tarsus** (Figs. 16.1 and 4). The tarsi terminate with paired claws. The setae of the legs may be smooth, plumose or pectinate, long and delicate, or short and spiniform.

Halacarids differ from other freshwater mites by a combination of the characters: (1) cuticular plates present, but never strongly sclerotized (as in the Oribatida); (2) epimera I and II as well as epimera III and IV fused, these plates separated by a gap, accordingly leg pairs I and II directed forward, leg pairs III and IV backward; (3) no more than five pairs of gland pores and seven pairs of idiosomal setae on the dorsum; (4) palps with four articles; and (5) legs of adults have six articles.

MATERIAL PREPARATION AND PRESERVATION

Halacarid mites should be preserved and stored in 70% ethanol. Fixatives such as formalin make the mites difficult to clear.

Reliable identification of halacarid mites requires microscopic examination. Specimens can be examined in a drop of glycerine, but for species level identification must be cleared and slide mounted. Halacarids are typically cleared in pepsin or lactic acid, and gentle warming (40–50°C) may facilitate the process. The gnathosoma is then removed using a sharp needle, and the body contents are squeezed out with help of gentle pressure using a blunt needle.

Cleared specimens can be mounted for study and permanent storage in glycerine jelly or Hyrax. After initial hardening of the mounting medium, the coverslip should be ringed using a standard microscopical sealing agent. Berlese's medium, modified Hoyer's fluid, polyvinyl lactophenol, or glycerine can be used for temporary mounts. Specimens cleared in lactic acid must be rinsed to prevent formation of crystals in the mounting medium. Staining with chlorazol black often facilitates the interpretation of morphological structures in overcleared specimens.

Mounting specimens between two cover slips is recommended to facilitate examination of both dorsal and ventral surfaces. These preparations can be stored in metal slide frames or attached to a glass slide using a drop of glycerine.

KEYS TO HALACARIDAE

Arachnida: Acari: Halacaridae: Genera

1 Anterior and posterior dorsal plate separated; pair of ocular plates large (Fig. 16.1) 2

1′ Anterior and posterior dorsal plate fused to a shield; ocular plates tiny (Fig. 16.14)..... *Ropohalacarus uniscutatus* Bartsch, 1982 [Holarctic. Australia]

2(1) Palps attached laterally to gnathosoma; interval between first palpal articles larger than articles' width and major part of first palpal articles visible in ventral aspect (Fig. 16.2) 3

2′ Palps attached dorsally to gnathosoma; interval between first palpal articles smaller than articles' width and first palpal article (almost) completely masked in ventral aspect (Fig. 16.24)..... 6

3(2) Third palpal article with short medial spur or seta (Fig. 16.2); dorsal plate ornamentation uniform, foveate or reticulate (Figs. 16.1 and 8); epimeral pores small (diameter ≤5 μm) or absent 4

3′ No spine or seta on third palpal article (Fig. 16.17); posterior dorsal plate with distinctly or faintly delimited costae, which have an ornamentation different from remainder of plate (Fig. 16.15); epimeral pores distinct (diameter 10−25 μm) with numerous protruding tines (Fig. 16.16) ..... ***Copidognathus***

4(3) Second palpal article with one seta, situated in distal half; tarsus I with 3−5 ventral setae and apical pair of parambulacral setae (Fig. 16.19) 5

4′ Second palpal article with two setae, one in basal, one in distal half (Fig. 16.2); tarsus I with single ventromedial seta and apical pair of parambulacral setae (Fig. 16.5) ..... ***Porohalacarus***

5(4) Idiosoma anterior margin rounded or truncate; ventral plates separate; genu I shorter than telofemur I ..... ***Halacarellus/Troglohalacarus***

5′ Idiosoma with anterior spine (Fig. 16.21); ventral plates fused; genu I longer than telofemur I (Fig. 16.20) ..... *Lobohalacarus weberi* (Romijn & Viets) [Cosmopolitan]

6(2) Four or five pairs of gland pores, two posterior pairs in striated integument lateral to posterior dorsal plate (Fig. 16.8); genital acetabula situated outside genital opening, on genital plate (or in striated integument); third palpal article with stout spine (Figs. 16.10 and 25) 7

6′ Gland pores small or inconspicuous, two posterior pairs, if present, situated on posterior dorsal plate (Fig. 16.22); genital acetabula inside genital opening or on genital sclerites (Fig. 16.3); third palpal article without spine or seta (Figs. 16.26 and 27) 11

7(6) Anal sclerites size ∼0.5 genital sclerites; genital acetabula situated lateral and posterior to genital opening (Fig. 16.11) 8

7′ Anal sclerites much smaller than genital sclerites (Fig. 16.23); genital acetabula situated lateral and anterior to genital opening, along lateral margins of genital plate ..... ***Limnohalacarus***

8(7) Second palpal article with two setae (setae length may be unequal); rostrum basal half with basal pair of maxillary setae (Fig. 16.25) 9

8′ Second palpal article with single seta; rostrum apical half with both pairs of maxillary setae ..... ***Parasoldanellonyx***

9(8) Genu and tibia II ventral spines wide and coarsely bipectinate (Fig. 16.35, arrows) 10

9′ Genu and tibia II ventral spines either slender and faintly bipectinate or spiniform but never coarsely bipectinate ..... ***Soldanellonyx***

10(9) Surface of idiosomal plates, gnathosomal base, palps and legs conspicuously reticulate; telofemur II length <1.5 height ..... *Himejacarus morimotoi* Irimura, 1957 [Japan]

10′ Surface of dorsal plates reticulate, no marked reticulation on legs and gnathosoma; telofemur II length >2x height ..... *Stygohalacarus scupiensis* Viets, 1934 [Macedonia]

11(6) Posterior epimeral plate with a dorsal and three ventral setae; second palpal article with two setae (Fig. 16.26), fourth palpal article basally with a spur and two setae ..... ***Lohmannella***

11′ Posterior epimeral plate with a dorsal, marginal, and ventral seta; second palpal article with one seta (Fig. 16.27), fourth palpal article basally with three slender setae but no spur ..... *Porolohmannella violacea* (Kramer, 1879) [Holarctic]

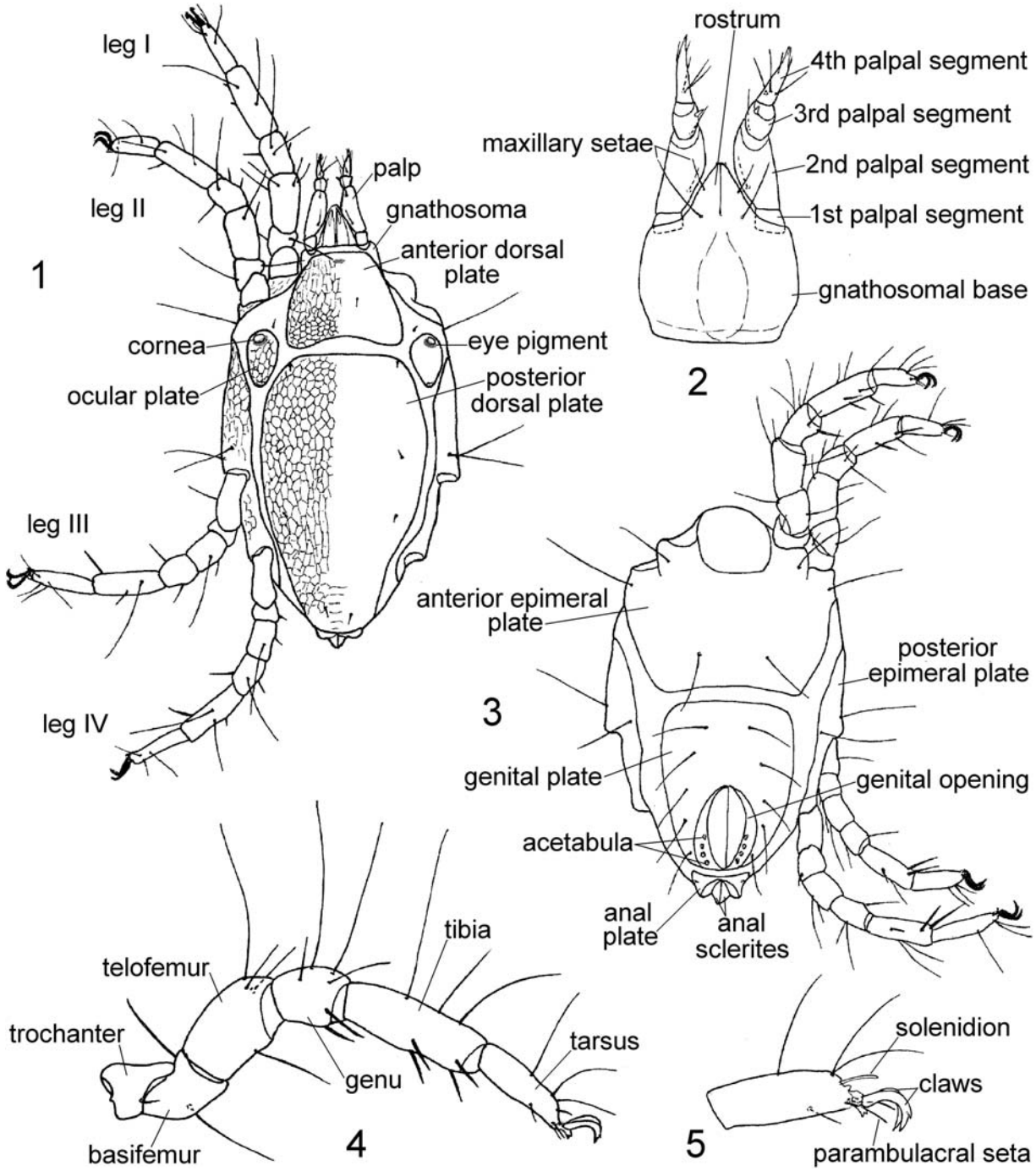


PLATE 1 **Figs. 16.1–5.** *Porohalacarus alpinus* (Thor), female. **Fig.** 16.1, idiosoma with gnathosoma and legs, dorsal; **Fig.** 16.2, gnathosoma, ventral; **Fig.** 16.3, idiosoma with gnathosoma and legs, ventral; **Fig.** 16.4, leg I, medial; **Fig.** 16.5, tarsus I, lateral.

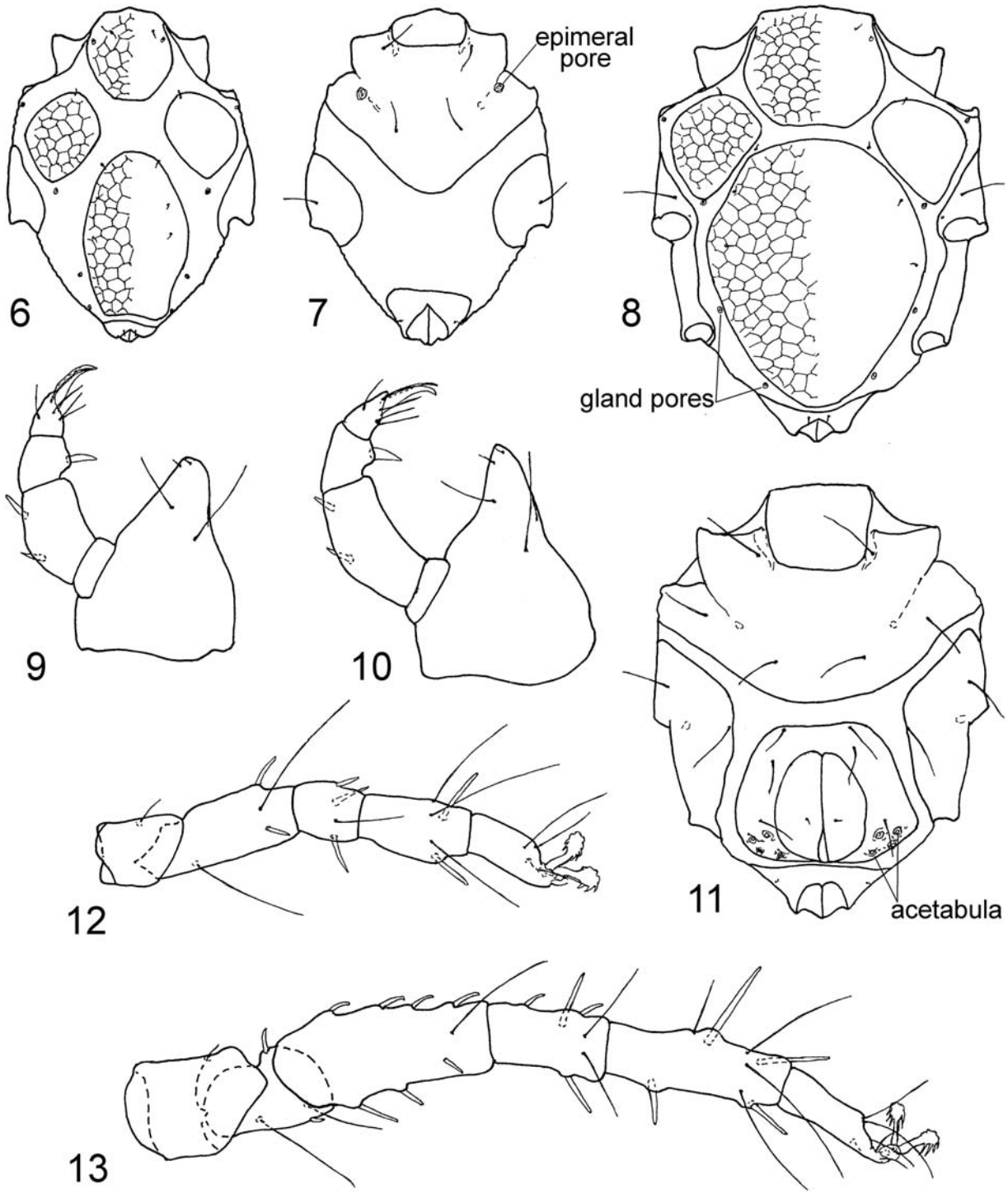


PLATE 2 **Figs. 16.6–13.** *Soldanellonyx chappuisi* Walter, larva and female. **Fig.** 16.6, idiosoma, larva, dorsal; **Fig.** 16.7, idiosoma, larva, ventral; **Fig.** 16.8, idiosoma, female, dorsal; **Fig.** 16.9, idiosoma, female, ventral; **Fig.** 16.10, gnathosoma, larva, lateral; **Fig.** 16.11, gnathosoma, female, lateral; **Fig.** 16.12, leg I, larva, dorsal; **Fig.** 16.13, leg I, female, dorsal.

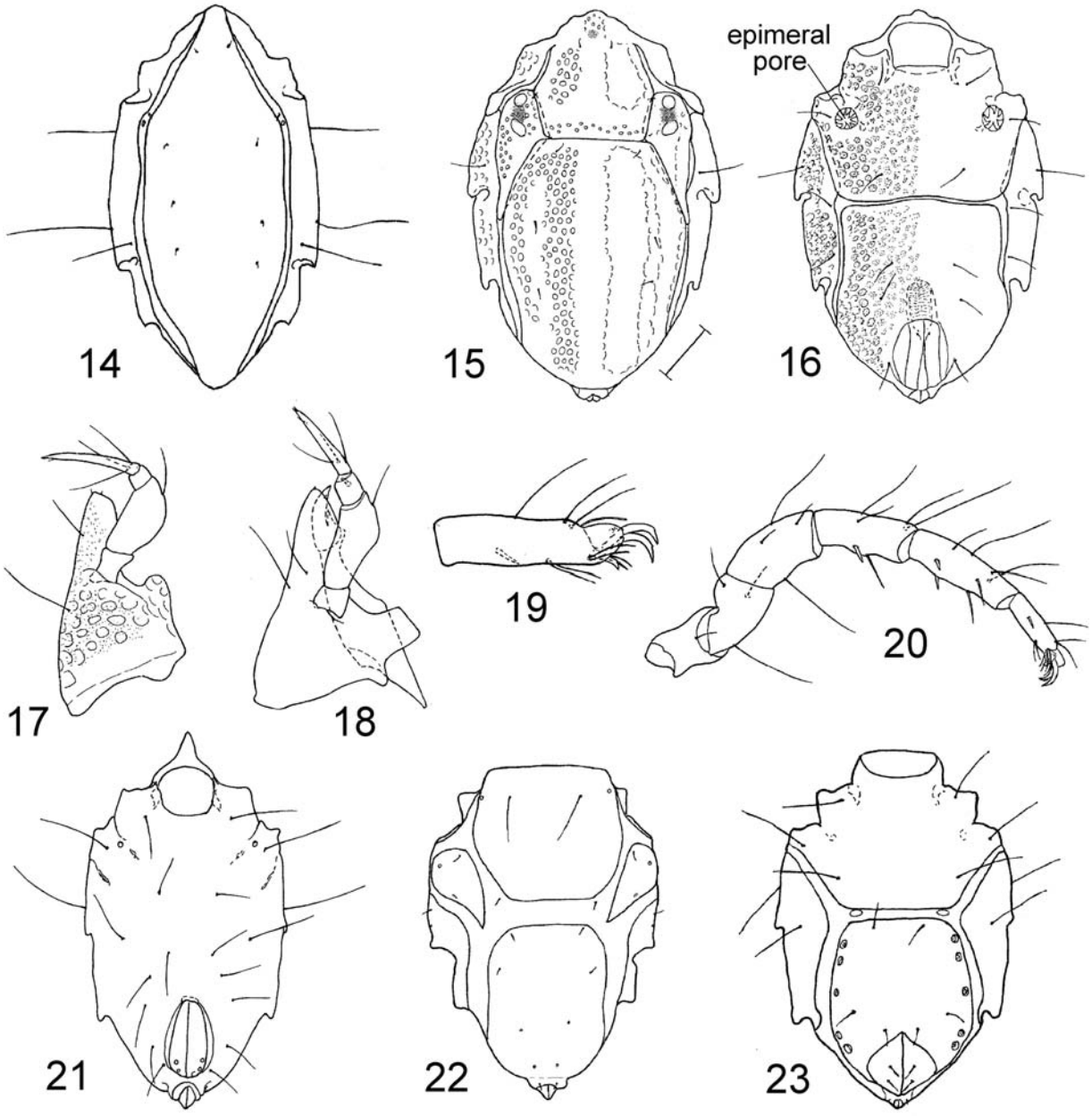


PLATE 3 **Figs. 16.14–23.** *Ropohalacarus uniscutatus* (Bartsch) *Copidognathus tectiporus* (Viets) *Lobohalacarus weberi* (Romijn & Viets), *Lohmannella stammeri* Viets, *Limnohalacarus cultellatus* Viets. **Fig.** 16.14, *Ropohalacarus uniscutatus*, female, idiosoma, dorsal; Figs. 16.15–17, *Copidognathus tectiporus*, female, **Fig.** 16.15, idiosoma, dorsal; **Fig.** 16.16, idiosoma, ventral; **Fig.** 16.17, gnathosoma, lateral; Figs. 16.18–21, *Lobohalacarus weberi*, female, **Fig.** 16.18, gnathosoma with chelicera, lateral; **Fig.** 16.19, tarsus I, lateral; **Fig.** 16.20, leg I, medial; **Fig.** 16.21, idiosoma, ventral; **Fig.** 16.22, *Lohmannella stammeri*, female, idiosoma, dorsal; **Fig.** 16.23, *Limnohalacarus cultellatus*, female, idiosoma, ventral.

Arachnida: Acari: Halacaridae: *Copidognathus*: Species

1 Anterior and posterior dorsal plates with distinctly delimited porose areolae; areolae with rosette pores; ocular plates with corneae and distinct dark eye spots 2

1′ Anterior dorsal plate without, posterior dorsal plate with faintly delimited reticulate costae; ocular plates lack corneae and dark eye spots ..... *Copidognathus profundus* (Viets. 1936)
[Macedonia (Lake Ohrid)]

2(1) Telofemur I length 1.7−1.8x height 3

2′ Telofemur I length 2.2x height ..... *Copidognathus dactyloporus* Benfatti, Mari & Morselli, 1989
[Italy]

3(2) Epimeral pores diameter 13−15 μm ..... *Copidognathus hephaestios* Benfatti, Mari, & Morselli, 1992
[Italy]

3′ Epimeral pores diameter 20−25 μm ..... *Copidognathus tectiporus* (Viets, 1936)
[Bulgaria, Germany, Macedonia, The Netherlands, Turkey, Ukraine]

Arachnida: Acari: Halacaridae: *Porohalacarus*: Species

1 Ocular plates length distinctly less than anterior dorsal plate (Fig. 16.1); anterior dorsal plate with truncate frontal margin; ventral plates separated ..... *Porohalacarus alpinus* (Thor, 1910)
[Cosmopolitan]

1′ Ocular plate length at least equal to anterior dorsal plate; anterior dorsal plate with small frontal spine; ventral plates fused ..... *Porohalacarus gallicus* (Migot, 1926)
[France, United Kingdom]

Arachnida: Acari: Halacaridae: *Halacarellus* and *Troglohalacarus*: Species

1 Basifemur I with slender ventral seta, length > basifemur diameter; genital acetabula not masked by genital sclerites (Fig. 16.30) 2

1′ Basifemur I with short ventral spine (Fig. 16.28, arrow), spine length < basifemur diameter; genital acetabula within genital opening and masked by genital sclerites (Fig. 16.29); near shore groundwater ..... *Halacarellus phreaticus* Petrova, 1972
[Black Sea, Mediterranean regions]

2(1) Telofemur I with 2−3 ventral setae, 1−2 of them spiniform 3

2′ Telofemur I with single, slender ventral seta ..... *Halacarellus hyrcanus* (Viets, 1928)
[Caspian and Black Sea and rivers emptying into these basins; rivers Elbe, Rhine]

3(2) Tibia I with two pairs of ventral setae; tibia II with four ventral setae, three of them short and ventromedial ..... *Halacarellus fontinalis* Bartsch & Gerecke, 2011
[Austria]

3′ Tibia I with three pairs of ventral setae, two basal pairs spiniform; tibia II with three short ventral setae, two of them in ventromedial position ..... *Troglohalacarus dentipes* Viets, 1937
[Spain]

Arachnida: Acari: Halacaridae: *Limnohalacarus*: Species

1 Ocular plate and sclerite with third pair of gland pores separated (Fig. 16.34); ventral plates separated (Fig. 16.23) 2

1′ Ocular plate and sclerite with third pair of gland pores fused; ventral plates fused 5

2(1) Claw I with long tines (Fig. 16.32), without separate ventral process 3

2′ Claw I apically with delicate tines, basally with ventral process (Fig. 16.33, arrow) 4

3(2) Ocular plate with cornea; tibia IV ventral setae slender and smooth ..... *Limnohalacarus wackeri* (Walter, 1914)
[Widespread]

3′ Cornea lacking; tibia IV with one ventroapical setae barbed ..... *Limnohalacarus capernaumi* Petrova, 1966
[Israel]

4(2) Tibia IV ventral setae slender and smooth ..... *Limnohalacarus cultellatus* Viets, 1940
[Cosmopolitan]

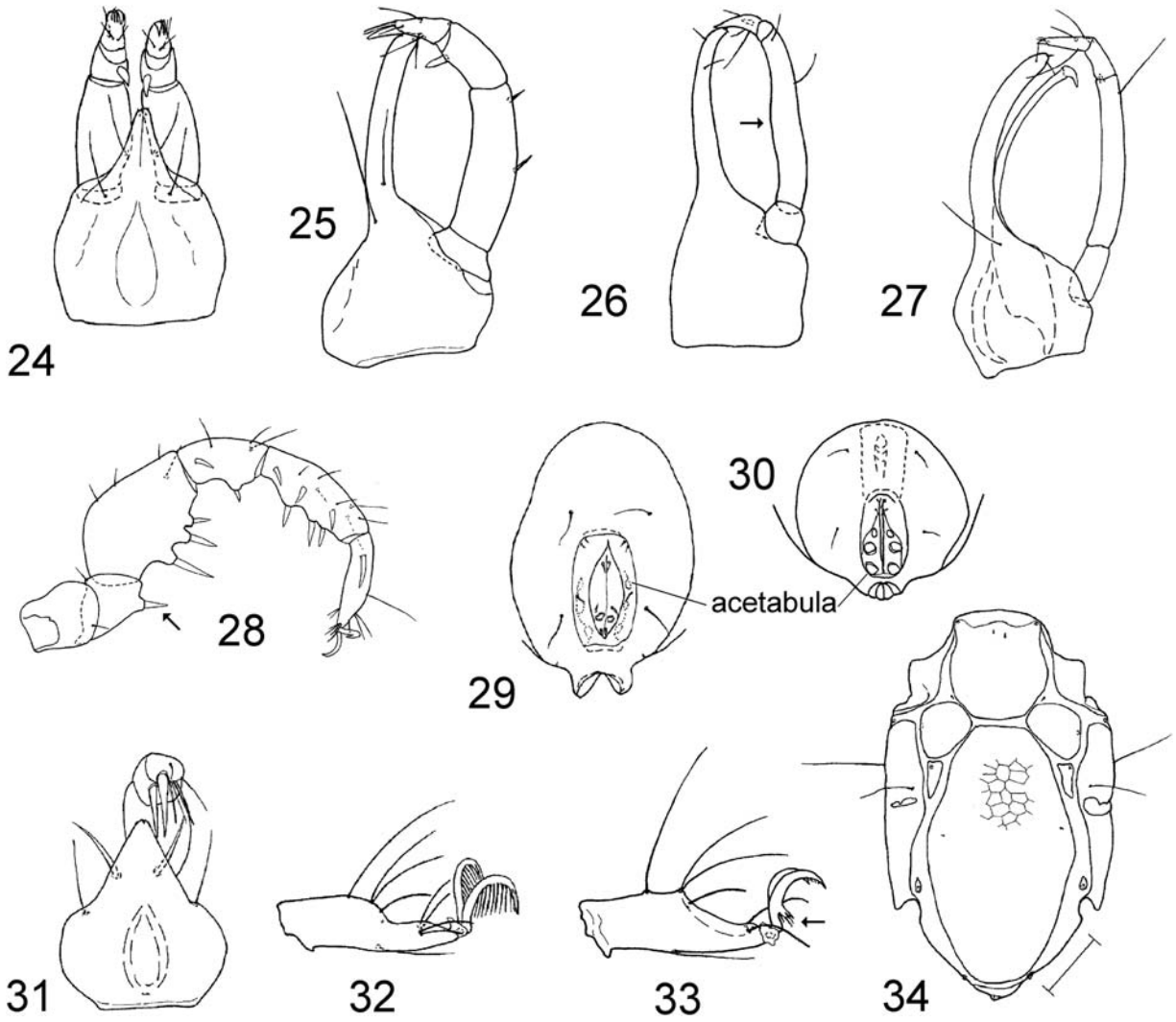


PLATE 4 **Figs. 16.24–34.** *Soldanellonyx chappuisi* Walter, *S. lohmannelloides* (Sokolov & Yankovskaya), *Lohmannella stammeri* Viets, *Porolohmannella violacea* (Kramer) *Halacarellus hyrcanus* (Viets) *H. phreaticus* Petrova, *Limnohalacarus cultellatus* Viets, *L. dentatus* Bartsch, *L. wackeri* (Walter) **Fig.** 16.24, *Soldanellonyx chappuisi*, female, gnathosoma, ventral; **Fig.** 16.25, *Soldanellonyx lohmannelloides*, female, gnathosoma, lateral; **Fig.** 16.26, *Lohmannella stammeri*, female, gnathosoma, lateral; **Fig.** 16.27, *Porolohmannella violacea*, female, gnathosoma with chelicera, lateral; **Figs.** 16.28 and 29, *Halacarellus phreaticus*, female, **Fig.** 16.28, leg I, medial; **Fig.** 16.29, genitoanal plate, genital acetabula masked by genital sclerites, several genital spines of ovipositor visible; **Fig.** 16.30, *Halacarellus hyrcanus*, female, genitoanal plate; **Fig.** 16.31, *Limnohalacarus dentatus*, female, gnathosoma, ventral; **Fig.** 16.32, *Limnohalacarus wackeri*, female, tarsus I; **Figs.** 16.33 and 34, *L. cultellatus*, female, **Fig.** 16.33, tarsus I, lateral; **Fig.** 16.34, idiosoma, dorsal.

4′	Tibia IV with one ventroapical seta barbed	*Limnohalacarus inopinatus* Fain & Lambrechts, 1987 [Belgium (aquarium with warmwater fish)]
5(1)	With eye pigment; both pairs of maxillary setae slender	*Limnohalacarus mamillatus* Fain & Lambrechts, 1987 [Australian and Neotropical bioregions. Belgium (aquarium with warmwater fish)]
5′	No eye pigment present; maxillary setae apical pair wider than basal pair (Fig. 16.31)	*Limnohalacarus dentatus* Bartsch, 2013 [Germany (aquarium with warmwater fish)]

Arachnida: Acari: Halacaridae: *Lohmannella*: Species

1	Tarsus I with 1–2 spiniform ventral setae (Fig. 16.36); anteriorly arched, posteriorly tapering (Fig. 16.22)	2
1′	Tarsus I without ventral setae; ocular plates rhomboid	*Lohmannella andrei* (Angelier, 1951) [France]

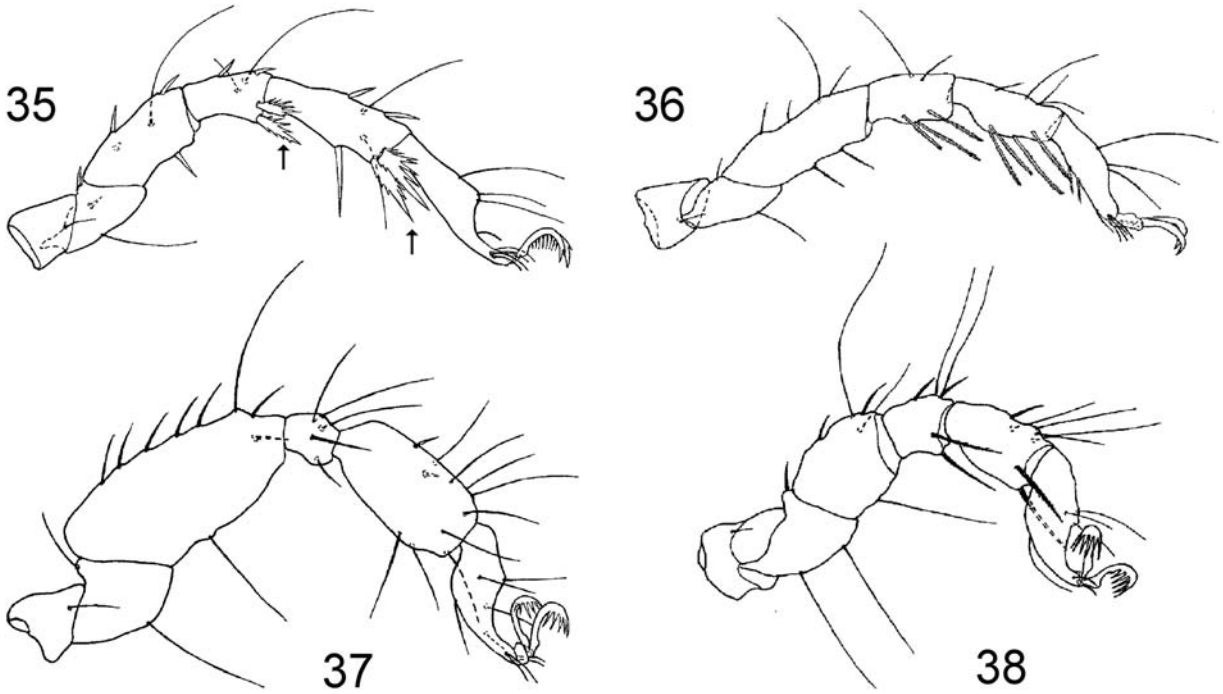


PLATE 5 **Figs. 16.35–38.** *Stygohalacarus scupiensis* Viets, *Lohmannella stammeri* Viets, *Parasoldanellonyx parviscutatus* (Walter), *Soldanellonyx monardi* Walter. **Fig.** 16.35, *Stygohalacarus scupiensis*, female, leg I, medial; **Fig.** 16.36, *Lohmannella stammeri*, female, leg I, medial; **Fig.** 16.37, *Parasoldanellonyx parviscutatus*, female, leg I, medial; **Fig.** 16.38, *Soldanellonyx monardi*, female, leg I, medial.

2(1)	Tibia and genu I with four and three spiniform ventral setae, respectively	3
2′	Tibia and genu I with six and four spiniform ventral setae, respectively	4
3(2)	Telofemur II with two ventral bristles; second palpal article with curved ventral margin (Fig. 16.26, arrow) ..... *Lohmannella stammeri* Viets, 1939 [Italy, Montenegro]	
3′	Telofemur II without ventral bristles; second palpal article with almost straight ventral margin ..... *Lohmannella heptapegoni* (Petrova, 1966) [Israel]	
4(2)	Telofemur I with one ventral bristle ..... *Lohmannella curvimandibulata* (Petrova, 1969) [Bulgaria]	
4′	Telofemur I with two ventral bristles ..... *Lohmannella cvetkovi* (Petrova, 1965) [Bulgaria]	

Arachnida: Acari: Halacaridae: *Parasoldanellonyx*: Species

1	Tibia I length 2.8–2.9x genu I (Fig. 16.37)	2
1′	Tibia I length 1.9x genu I ..... *Parasoldanellonyx baicalensis* Sokolov, 1952 [Russia (Lakes Baikal and Khovsgol)]	
2(1)	Eye pigment beneath ocular plate; posterior dorsal plate width < anterior dorsal plate width; gnathosoma length and width subequal; rostrum triangular in ventral aspect ..... *Parasoldanellonyx parviscutatus* Walter, 1917 [Holarctic]	
2′	Eye pigment lacking; posterior dorsal plate width > anterior dorsal plate; gnathosoma length 1.3x width; rostrum elongate, narrowed anteriorly ..... *Parasoldanellonyx typhlops* Viets, 1933 [Palaearctic]	

Arachnida: Acari: Halacaridae: *Soldanellonyx*: Species

1 Telofemur I length <1.5x height; tibia I short, with two slightly spiniform ventral setae (Fig. 16.38) 2

1′ Telofemur I length >2.0x height; tibia I long, with four ventral spines (Fig. 16.13) 3

2(1) Anterior dorsal plate length ≥ width, and its length ~0.5 posterior dorsal plate; palps without marked reticulation ..... *Soldanellonyx monardi* Walter, 1919
[Cosmopolitan]

2′ Anterior dorsal plate wider than long, length 0.4x posterior dorsal plate; palps reticulate ..... *Soldanellonyx miyakoensis* Imamura, 1957
[Japan, Russia (Kamchatka)]

3(1) Gnathosoma length <1.5x width (Fig. 16.24) 4

3′ Gnathosoma length 2.1x width (Fig. 16.25) ..... *Soldanellonyx lohmannelloides* (Sokolov & Yankovskaya, 1970)
[Russia (Lake Baikal)]

4(3) Integument of plates reticulate, between plates striated, none with epicuticular tubercles; ocular plate shorter than anterior dorsal plate 5

4′ Integument of idiosoma, gnathosoma, and legs covered with minute tubercles; ocular plate longer than anterior dorsal plate ..... *Soldanellonyx papillosus* Imamura, 1957
[Japan]

5(4) Palp second article with basal seta at 0.3 of article length (from basal to apical) 6

5′ Palp second article with basal seta at 0.5–0.7 of article length 7

6(5) Anterior dorsal plate length: width ratio 1:0.9; posterior dorsal plate length 1.4x width ..... *Soldanellonyx morimotoi* Imamura, 1970
[Japan]

6′ Anterior dorsal plate width and length subequal; posterior dorsal plate length 1.6x width ..... *Soldanellonyx visurgis* Viets, 1959
[Holarctic. Oriental Region]

7(5) Palp second article length 2x width; tarsus I length 4–5x height 8

7′ Palp second article length 1.5x width; tarsus I length 6x height ..... *Soldanellonyx akiyoshiensis* Imamura, 1957
[Japan]

8(7) Palp second seta at 0.5 of its length (from basal to apical); female genital acetabula on genital plate ..... *Soldanellonyx chappuisi* Walter, 1917
[Holarctic]

8′ Palp second seta at 0.7 of its length (from basal to apical); female with several genital acetabula in striated integument outside genital plate ..... *Soldanellonyx biwaensis* Tuzovskij, 2011
[Japan]

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Chapter 16.1

Arthropoda: Introduction to Crustacea and Hexapoda

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Introduction to the Subphylum Crustacea

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INTRODUCTION

Within the Arthropoda recent molecular, morphological, and paleontological studies have suggested many classification hypotheses that upend traditional views. The preponderance of evidence demonstrates that the Hexapoda (Apterygota + Insecta) represent a clade nested within the Crustacea (Reiger et al., 2005). This Crustacea + Hexapoda clade has been referred to as "Tetraconata" or "Pancrustacea" (Reiger et al., 2005; Oakley et al., 2013), and this nomenclature was followed in the Thorp & Covich (4th edition) Volume I of the present series. However, in retrospect, we will treat the Crustacea + Hexapoda clade under the name "Crustacea." We think that creating a new nomen for a previously named clade just because some other clade is found to nest within it will only create confusion. Instead, we prefer to apply the principles of the International Code of Zoological Nomenclature (which does not officially apply to higher level taxonomy) and treat the Hexapoda as a class within the Crustacea, as would be done for lower taxonomic levels.

As relationships within the Crustacea are still unclear, we revert to a more traditional organization (Ahyong et al., 2011) for all categories encompassed within this clade.

TERMINOLOGY AND MORPHOLOGY

Hexapods and crustaceans are fundamentally separated by the position of the genitalia. In the crustaceans the genitalia

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are positioned between the thorax and the abdomen. Malacostracan males typically have the first pleopod pair (abdominal limbs) modified to transfer sperm from the thoracic gonopods to the female. The Hexapoda have the genitalia terminally positioned at the end of the abdomen, often withdrawn internally.

KEYS TO CRUSTACEA

Crustacea: Classes

1	Genitalia positioned at posterior end of thorax; limbs present, more than three pairs; two pairs of antennae; free-living or parasitic; wings never present 2
1′	Genitalia positioned at abdominal terminus; limbs present or absent, if present, not more than three pairs (pseudolegs may be present in some larval dipterans and lepidopterans; one pair of antennae; wings present or absent ..... **Hexapoda (p. 570)**
2(1)	Thoracopods segmented, never lamellar carapace bivalved or not 3
2′	Thoracopods lamellar, not segmented (Figs. 16.2.1 G, H); carapace bivalved or not (Figs. 16.2.1 A–F, K–L); OR if thoracopods are segmented, then bivalved carapace greatly reduced (Fig. 16.2.1 M) ..... **Branchiopoda** [Chapter 16.2]
3(2)	Carapace not bivalved 4
3′	Carapace bivalved, enclosing entire animal (Figs. 16.3.1–8) ..... **Ostracoda** [Chapter 16.3]
4(3)	*Either* compound eyes present, *or* animals sessile, fused to substrate (barnacles) 5
4′	Compound eyes absent, only medial naupliar eye present (Figs. 16.4.1–2) ..... **Copepoda** [Chapter 16.4]
5(4)	Naupliar eye present, or if absent, then animal entirely enclosed in a fused exoskeleton, with a single distal opening (barnacles); telson and uropods always absent (Figs. 16.5.1–6) ..... **Thecostraca** [Chapter 16.5]
4′	Naupliar eye absent in adults, telson or pleotelson present, uropods present or absent (Figs. 16.6.1–13) .... **Malacostraca** [Chapter 16.6]

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Crustacea: Hexapoda

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INTRODUCTION

This chapter includes orders and families of Hexapoda (subclasses Insecta and Entognatha (Collembola)) in which one or more life stages are aquatic and adapted for survival under or on the water surface. Some license has been taken with Collembola to include most families that might be encountered near water. Not included are families of insects that live on or burrow into emergent aquatic vegetation, internal parasites of aquatic animals, and riparian families that are closely associated with water but do not inhabit it.

Ten insect orders contain aquatic or semiaquatic species. Five (Ephemeroptera, Odonata, Plecoptera, Trichoptera, and Megaloptera) are orders in which almost all species have aquatic larvae. The remaining five orders (Coleoptera, Diptera, Heteroptera, Lepidoptera, and Neuroptera) are primarily terrestrial, but contain a substantial number of families, genera, and species that have one or more life stages adapted for living in or beside aquatic environments.

Four aquatic orders (Ephemeroptera, Odonata, Plecoptera, and Hemiptera) have a hemimetabolous life cycle that includes three developmental stages: egg, larva (nymph), and adult. The term larva is used here instead of nymph or naiad to standardize usage in the text. The larva nearly always lives in the water, while the adult is nearly always terrestrial. The other aquatic insect orders (Coleoptera, Diptera, Lepidoptera, Megaloptera, Neuroptera, and Trichoptera) undergo a holometabolous life cycle that includes four developmental stages: egg, larva, pupa, and adult. A rich accounting of the biology and ecology of all aquatic insect orders may be found in Thorp & Rogers (2016). Balian et al. (2008) undertook the herculean task of compiling diversity and distributional information on freshwater aquatic species across the globe. This compendium of contributed papers should be consulted by those trying to understand the importance of animals to freshwater ecosystems.

To help others navigate common name usage within insects, those insects not of the order Diptera (true flies) should be named such that *flies* is attached to the modifier. For instance, *mayflies* is correct, not *may flies*. Those within the Diptera may have flies separated from the modifier, such as in black flies, one common name for Simuliidae.

LIMITATIONS

The family level keys emphasize aquatic larvae and adults with aquatic stages. Keys to eggs, Heteroptera larvae, pupae, and terrestrial stages of aquatic species are not included. Earlier editions of Merritt et al. (2008) provided order, family, and generic keys for North America and was an inspiration for several works in Europe and the rest of the Palaearctic. Nilsson (1996A, 1997) presented a compendium of keys to adult and immature stages of aquatic insects in northern Europe. Depending upon the state of the knowledge of a particular group, keys were provided to the genus or species level for both larvae and adults. Kriska (2014) provided generic level keys to adult and immature aquatic insects of central Europe. Morse et al. (1994) contributed greatly by providing a manual for aquatic insect larval identifications in China. Much fragmentary, primary literature has come out of the entire area. More work remains to associate larval forms with adults and to compile this information into formats suitable for nonspecialist use.

TERMINOLOGY AND MORPHOLOGY

Morphological terms used for identification of aquatic insects vary somewhat among orders, but several terms are used in common. A plecopteran larva (Figs. 16.1.1 and 2) is used to illustrate these terms. Insects have three body regions: head, thorax, and abdomen. Dorsally, the head has a pair of antennae, a pair of compound eyes, and up to three **ocelli** or simple eyes. On the head are several mouthparts, including a **labrum**, a pair of mandibles, a pair of maxillae, and a **labium**. The **mandibles** are usually heavily sclerotized, toothlike structures, but might be modified in other orders for piercing or sucking of plant or animal body fluids. The **maxillae** and **labium** are usually multiarticulate and frequently have a pair of elongate **palps**.

The thorax is immediately posterior to the head and consists of three large segments: **prothorax** (anterior), **mesothorax,** and **metathorax** (posterior), which may be abbreviated as **Th1**, **Th2**, and **Th3**. In some orders, these segments may be combined so that individual segments are not visible. The dorsal sclerite of each segment is referred to as a **notum** (plural nota) or **tergum** (terga), the ventral sclerite as a **sternum** (sterna), and the lateral sclerites as **pleura** (singular pleuron). The reader may see in use pro-, meso-, and metanota as well as pro-, meso, or metasterna. Each thoracic segment has a pair of legs, each leg being divided into five parts: a **coxa** (plural coxae), **trochantin**, **femur** (femora), **tibia** (tibiae), and **tarsus** (tarsi). The femur and tibia are usually elongate and the tarsus has from one to five segments, depending on the order. The terminal tarsal segment often has one or two claws. In hemimetabolous insect larvae, wingpads (developing wings) are present dorsally on the meso- and metathorax, though some insects lack one or both wingpads, the latter resulting in wingless adults. Holometabolous aquatic immatures display wingpads only in the pupal stage.

The abdomen shares the same sclerite arrangement as the thorax, but may lack pleura in one or all segments within some groups. Up to 10 visible segments may be found on the abdomen; they are numbered consecutively from anterior to posterior, e.g., **Ab1 through Ab10**. Other orders may have fewer abdominal segments. Terminal abdominal appendages vary widely or may be absent; **cerci** (singular cercus) are present in several orders. In some orders, gills of various types may be present on the abdomen, but they may also be located on the thorax, or even on the head.

MATERIAL PREPARATION AND PRESERVATION

Preservative type depends on the intended use of the specimens. Typically, aquatic insects with high water content in their bodies are best preserved in fluid, but adults of

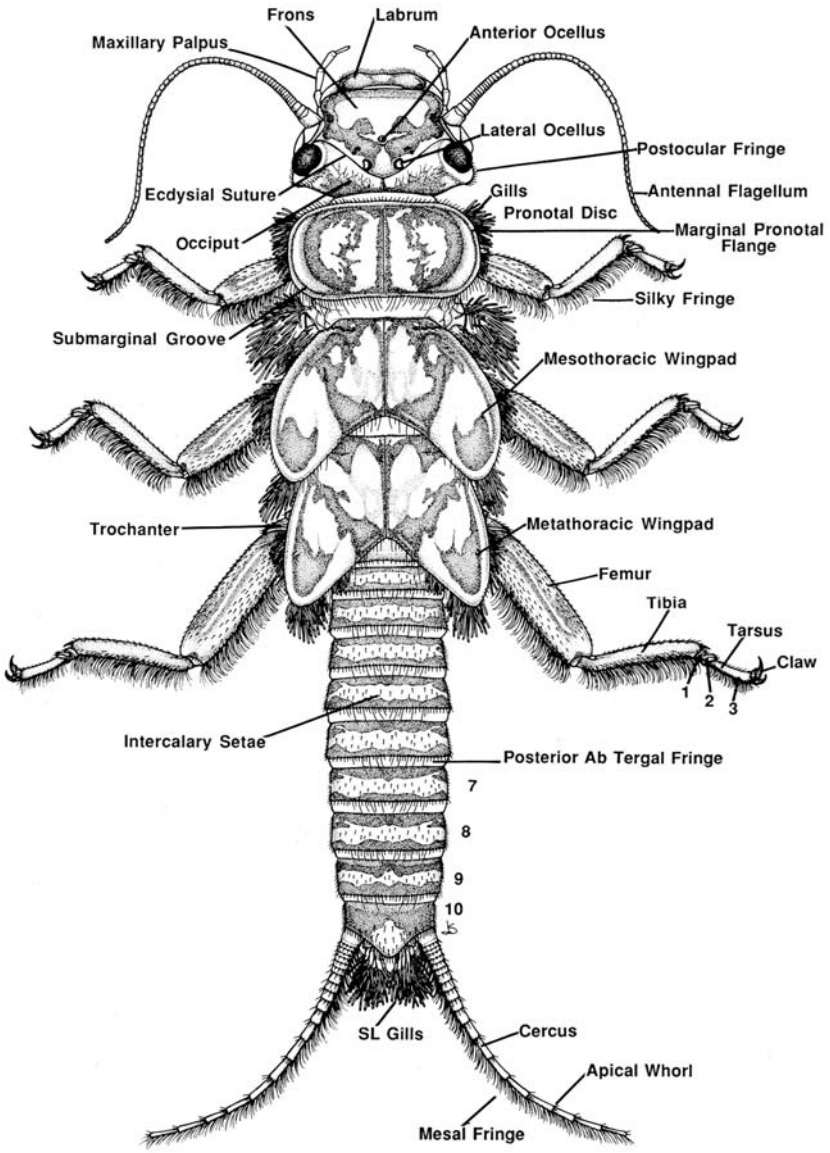


FIGURE 16.1.1 Plecoptera, Perlidae, generalized habitus (dorsal). *Modified from Stewart & Stark (2002).*

Coleoptera, some Diptera, Hemiptera, Lepidoptera, Odonata, and Trichoptera are often pinned or stored in envelopes, especially if colored hair patterns will be lost in ethanol—more on this to follow. If DNA is to be extracted, whole specimens are best put into 95%−100% ethanol, ground alive into RNA buffer (e.g., for transcriptomes), or frozen in liquid nitrogen or on dry ice. Consult a colleague who works with the type of nucleic acids you desire to obtain for best instructions. High concentrations of ethanol leave specimens brittle and difficult to manipulate without damage. A concentration of 70%−80% ethanol is preferable for teaching, reference collections, or life history study measurements. A less expensive alternative is the use of 5%−10% buffered formalin or Kahle's fluid. These are fixatives that create cross bridges in proteins, resulting in supple specimens that also retain internal structures better than those in ethanol. However, they require more careful storage and disposal, and are not desirable for permanent storage (move to 70% ethanol). Other fixatives and preservatives for aquatic specimens are reported elsewhere (Smith, 2001). Permanent storage of aquatic larvae and most adults should be in at least 70%−80% ethyl alcohol (EtOH). All waste ethanol and fixatives with formalin or other toxic materials should be considered chemical waste and treated properly. Certainly, this discussion of preservative/fixative techniques should be augmented with further reading.

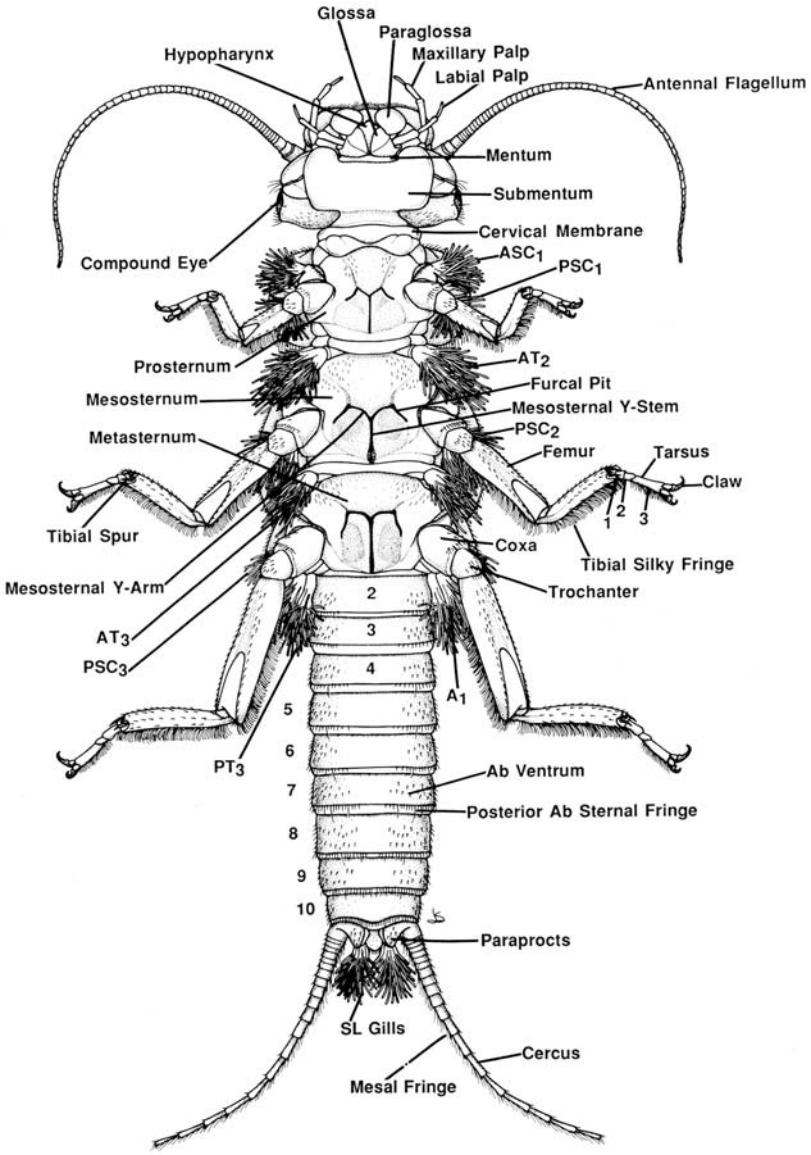


FIGURE 16.1.2 Plecoptera, Perlidae, generalized habitus (ventral). *Modified from Stewart & Stark (2002).*

The type of long-term storage container used is extremely important in protecting your investment in the specimens. The specimens may be reused for other purposes and the identity checked—every determination is an assertion of the identifier, and in our experience determinations are frequently wrong, incomplete, or the name needs to be updated due to synonymy or revision. Part of reproducibility of your work is being able to reexamine voucher specimens!

Substandard storage may result in desiccation of specimens. Natural history museums whose specimens need to last for centuries use a variety of wet storage methods. One involves the use of bail jars or large screwcap, wide-mouthed jars as storage for many smaller units. Specimens are placed in 10 mL or larger shell vials with labels enclosed, filled to the top with ethanol, and the top stoppered tightly with cotton. The jar is then flooded with ethanol to a level well above the shell vials. In this way, all specimens from a sample, specimens of a given species, or species within a genus may be stored in the same container. One drawback is difficulty finding a particular specimen within jar. A positive outcome is that jars may be examined rapidly and addition ethanol added to maintain a constant level.

Another storage method is to use 5–10 mL, glass patent lip vials with neoprene, or rubber, stoppers. Museums usually place these vials in linear racks and organize by taxon name. The racks are stored in a steel vial cabinet. Smaller institutions and private collections often group vials in cardboard unit trays with grid insets. Smaller cabinets may be used with drawers in which the unit trays may be placed. Regardless of cabinet type, stoppered storage was the gold standard for most of the 20th century. Unfortunately, high-quality stoppers are now nearly impossible to obtain. The available neoprene stoppers tend to become hard and the bases often swell in ethanol, making them difficult to remove and reuse. Some stoppers bleed color as well. Nearly all stoppers purchased recently will require replacement approximately every two decades. They must be watched diligently for evaporation.

Screw cap vials with beveled polyethylene inserts are great alternatives to patent lip vials. Three- (~10 mL) and four-dram (~16 mL) sizes are typical for storage of insect specimens, the latter being large enough for nearly all aquatic insects. We use both. Three dram screw cap vials are often not wide enough to pass standard forceps to the bottom (obtain slim forceps), but they do take up less room than four-dram vials. Screw cap vials with flat paper or plastic liners and shell vials that are stoppered with cork or plastic snap caps should be avoided for long-term storage because of gradual to rapid evaporation of the ethanol. With much use, the plastic threads of snap caps are damaged and evaporation of alcohol begins.

Other wet storage is possible, and under some circumstances, preferable to those discussed herein. A host of plastic vials are available whose lids have neoprene liners that prevent evaporation. Vials come in a variety of sizes. Some use the 2-ml and 8-ml vials since they are great for cold storage (you cannot do this with stoppers, they shrink and lose seal). A variety of storage boxes are available. These may be stored in freezers to prolong DNA extraction.

Adult aquatic Coleoptera and Heteroptera are normally mounted on pins, but may be preserved in EtOH. Several specimens of a given species from a given site/date collection effort can be kept in a single vial to reduce storage space and curation time. Specialists collect adult Odonata into labeled paper triangles and then soak them in acetone. Acetone helps to preserve color and extracts fats that leave specimens looking greasy and dull. The specimen is then dried with wings folded above the thorax and stored in clear, glycine envelopes. A card of acid-free paper with location and determination information should be inserted into the envelope and the envelopes stored as index cards in a pest-proof container.

A dissecting microscope is used to examine most specimens. Wet specimens are examined in watch glass, Petri dish, or similar container, completely covered with ethanol. The use of a layer of very small glass beads or silica sand in the watch glass permits insects to be imbedded for viewing from any angle. For some fragile insects, especially mayflies, it may be better to crimp small fishing weights (called split shots) around minuten pins as anchors to keep specimens in place. Whole specimens are generally not slide mounted, with the exception of some Diptera larvae, but the mouthparts and other sections can be teased apart for viewing on slides, in glycerin, water, or alcohol. Additional reading will be necessary to learn specific tasks such as semipermanent mounting of Chironomidae (nonbiting midge) larvae for identification.

ACKNOWLEDGMENTS

We wish to thank the aquatic entomologists who came before us, who have built a substantial legacy for the future of our science. Important contributors who have influenced us include Peter Zwick, John C. Morse, Ding Yang, Ole Saether, Kenneth W. Stewart, R. W. Merritt, William L. Hilsenhoff, Lydia Zhiltzova, John Brittain, H. B. Noel Hynes, G. B. Wiggins, H. H. Ross, William P. (Pat) McCafferty, and many others. Some are still active, some are gone. We hope that their legacy spurs a new generation to continue taxonomy and all manner of study of aquatic insects in the future.

KEYS TO HEXAPODA

Crustacea: Hexapoda: Subclasses

1	Mouthparts internal; abdomen forked distally, and bent ventrally to meet the collophore (tubular projection) descending from the first abdominal segment; wings absent (Fig. 16.1.3)	Entognatha, subclass: **Collembola [p. 570]**
1′	Mouthparts external; abdomen various, collophore absent; wings present or not	**Insecta [p. 573]**

Crustacea: Hexapoda: Entognatha: Collembola: Families

Aquatic dependency of Collembola is difficult to document for the majority of species, most of which are primarily terrestrial. Deharveng et al. (2008) have summarized the available information, finding that four orders of Collembola—Entomobryomorpha, Neelipleona, Poduromorpha, and Symphypleona—have at least some hydrophilous species. They report that as of 2008 the Palaearctic was known to have at least 2100 valid collembolan

species, 406 of which were hydrophilous to some extent. Since all Palaearctic families of springtails could be encountered while sampling in and near freshwater habitats, they have been included in the key. This key is modified from that of Christiansen & Snider (2008). The complexity of characters required to separate Collembola families necessitates the use "in part" after several family names—some families key out in multiple locations in the key.

1	Body elongate; thorax and abdomen distinctly segmented (Fig. 16.1.3)	2
1′	Body somewhat globular or oval (Fig. 16.1.4)	11
2(1)	First thoracic segment visible dorsally, with dorsal setae (Fig. 16.1.5)	3
2′	First thoracic segment often not visible dorsally, without dorsal setae	5
3(2)	Dens absent or <2.5x as long as manubrium; mouthparts directed forward; furcula apex not distinctly convergent	4
3′	Dens >3x long as manubrium (Fig. 16.1.6); mouthparts directed downward; furcula apex distinctly convergent (Fig. 16.1.7)	Poduridae, one species: *Podura aquatica* Linnaeus, 1758
4(3)	Pseudocelli present; eyes always absent (Fig. 16.1.8)	Onychiuridae
4′	Pseudocelli absent; eyes present or rarely absent	Hypogastruridae
5(2)	Dens with spines (Figs. 16.1.9 and 10)	6
5′	Dens without spines	7
6(5)	Mucro short and bidentate (Fig. 16.1.9)	Isotomidae (in part)
6′	Mucro elongate with three or more teeth (Fig. 16.1.10)	Entomobryidae (in part)
7(5)	Body without scales	8
7′	Body with scales	Entomobryidae (in part)
8(7)	Postantennal organ absent	9
8′	Postantennal organ present or rarely absent (Fig. 16.1.11)	Isotomidae (in part)
9(8)	Abdominal segments 4–6 separate	10
9′	Abdominal segments 4 and 5 fused, segment 6 reduced	Actaletidae
10(9)	Antennae longer than head; eyes present	11
10′	Antennae shorter than head; eyes absent	Neelidae
11(10)	Body elongate oval; furcula short, 20% of body length, dens with three setae (Fig. 16.1.12)	Mackenziellidae
11′	Body globular; furcula long, near half body length, dens with numerous setae (Fig. 16.1.4)	Sminthuridae

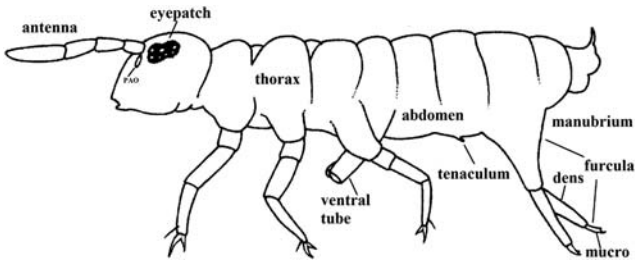


FIGURE 16.1.3 Generalized Collembola (lateral). *Modified from Christiansen & Snider, 2008.*

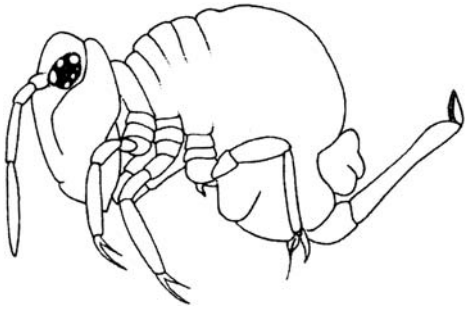


FIGURE 16.1.4 Sminthuridae, habitus (lateral). *Modified from Christiansen & Snider, 2008.*

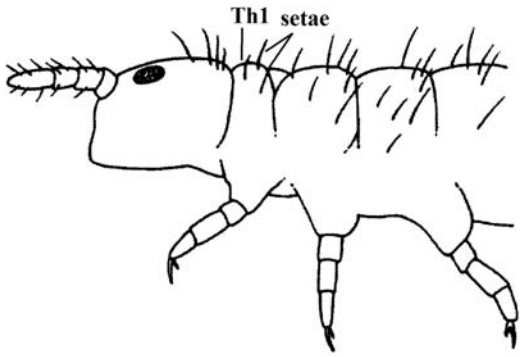


FIGURE 16.1.5 Collembolan with thoracic segment one (Th1) visible and setae, lateral. *Modified from Christiansen & Snider, 2008.*

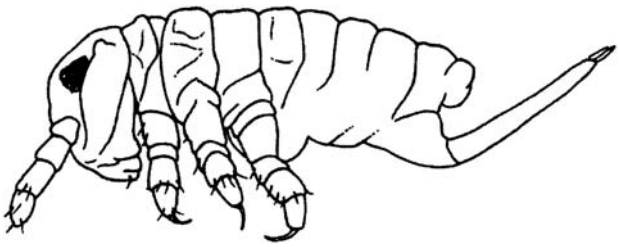


FIGURE 16.1.6 *Podura aquatica* Linnaeus (Poduridae) with dens 3x longer than mucro, lateral. *Modified from Christiansen & Snider, 2008.*

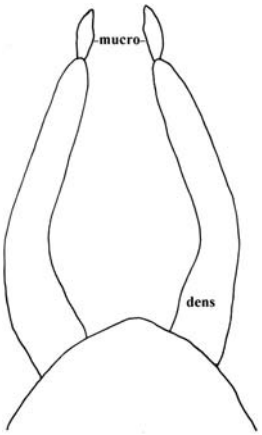


FIGURE 16.1.7 *Podura aquatica* Linnaeus (Poduridae) with dens convergent, dorsal view. *Modified from Christiansen & Snider, 2008.*

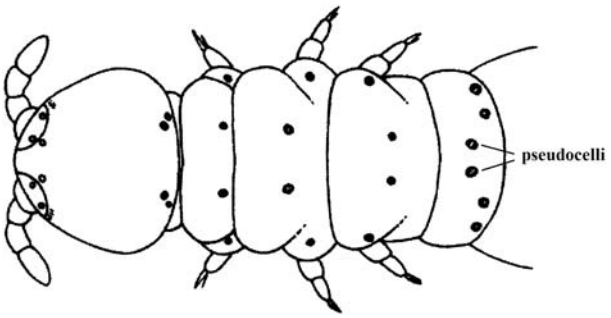


FIGURE 16.1.8 Onychiuridae with pseudocelli, dorsal. *Modified from Christiansen & Snider, 2008.*

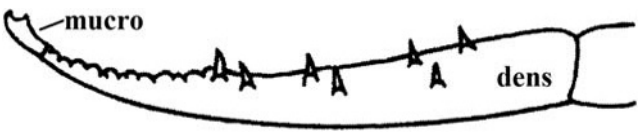


FIGURE 16.1.9 Isotomidae dens and mucro, ventrolateral. *Modified from Christiansen & Snider, 2008.*



FIGURE 16.1.10 Entomobryidae dens and mucro, ventrolateral. *Modified from Christiansen & Snider, 2008.*

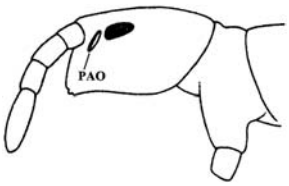


FIGURE 16.1.11 Isotomidae head with postantennal organ (PAO). *Modified from Christiansen & Snider, 2008.*

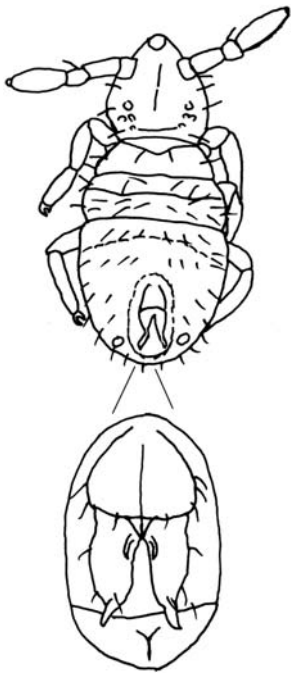


FIGURE 16.1.12 Mackenziellidae, habitus (dorsal). Inset of short dens with three setae. *Modified from Christiansen & Snider, 2008.*

Crustacea: Hexapoda: Insecta: Orders

l	Mummy-like, possibly encased in cocoon of silk (Lepidoptera, some Trichoptera), terrestrial cell (Megaloptera), or puparium (some Diptera, most Trichoptera) but may also be free (some Diptera); often with developing wings and legs appressed to or free from body ..... pupae (not keyed here)
l′	Not mummy-like, not encased in cocoon, cell, or puparium; legs and wings, if present, fully developed ..... larvae or adults 2
2(l)	Thorax with jointed legs (Fig. 16.1.1) 3
2′	Mobile larvae with prolegs, pseudopods, or creeping welts on one or more segments (Figs. 16.1.220, 226, 228, 235, 236, 238, and 247), or lacking (Figs. 16.1.241 and 246) ..... **Diptera [p. 630]**
3(1)	Large, functional wings present, forewings may be rigid and chitinized (Figs. 16.1.110, 112, and 124) or thickened in the proximal half (Figs. 16.1.97 and 100) 4
3′	Wingless (Figs. 16.1.91, 105, 146, 216, 175, 226) or with developing wingpads (Figs. 16.1.22, 24, 46, 66, 82, 91); if closely resembles Fig. 16.1.104, then go to couplet 5 6
4(3)	Mesothoracic wings rigid and chitinized (Figs. 16.1.112 and 127) or thickened in basal half (Figs. 16.1.97–100); also if closely resembling Fig. 16.1.104 5
4′	Meso- and metathoracic wings both membranous, with numerous veins ..... terrestrial adults (not keyed)
5(4)	Chewing mouthparts; mesothoracic wings as elytra, e.g., rigid and chitinized, covering metathoracic wings, elytra may be abbreviated (Figs. 16.1.112 and 127) ..... **Coleoptera [p. 601]**
5′	Sucking mouthparts formed into a broad or narrow tube (Figs. 16.1.92 and 94); mesothoracic wings hardened in basal half (Figs. 16.1.97–100), or lacking wings and closely resembling Fig. 16.1.104 ..... **Heteroptera** (in part) **[p. 595]**
6(3)	Two or three long, multisegmented filaments present at tip of abdomen (Figs. 16.1.22 and 82) 7
6′	Multisegmented appendages absent, or each appendage composed of only one or two segments (Figs. 16.1.40–42, 45, 105, 107, 143, 171, 215, and 219) 8
7(6)	Abdomen with plumose (Fig. 16.1.14), forked (Fig. 16.1.34), or lamellate gills, (Figs. 16.1.24 and 33); usually with two cerci and a median caudal filament, the latter occasionally reduce to few segments; tarsi with one claw (Fig. 16.1.15), one family with prothoracic claw split, appearing as two claws (Fig. 16.1.29) ..... **Ephemeroptera [p. 574]**
7′	Gills, if present, never lamellate, may be single or forked digitiform on head, thorax, and/or abdomen (Figs. 16.1.2, 72), or as clusters on neck, singly at mentum (Fig. 16.1.88), or on thorax (Fig. 16.1.89); two cerci, no median filament; tarsi with two claws (Fig. 16.1.86) ..... **Plecoptera [p. 590]**
8(6)	Extensible labium present (Figs. 16.1.60 and 61); abdomen terminating in three lamellae (Figs. 16.1.40 and 45), five usually short, triangular points (Fig. 16.1.41), or as blunt structure (Fig. 16.1.42) ..... **Odonata [p. 581]**
8′	Extensible labium absent; abdomen not terminating in lamellae or points 9
9(8)	Mouthparts sucking, formed into a broad or narrow tube (Figs. 16.1.92 and 94) or a pair of long stylets (Fig. 16.1.107) or otherwise elongate (Figs. 16.1.108 and 109) 10
9′	Mouthparts not sucking, not formed into a tube or pair of stylets 11
10(9)	Mouthparts a pair of long stylets (Fig. 16.1.107), or long mandibles (Fig. 16.1.109), or mandible long and hooked at tip (Fig. 16.1.108); all tarsi with one claw ..... **Neuroptera [p. 599]**
10′	Free-living; mouthparts a broad or narrow tube (Figs. 16.1.92 and 94); mesotarsi with two claws (Figs. 16.1.100 and 101) ..... **Heteroptera** (in part) **[p. 595]**
11(9)	Ventral prolegs on Ab3–6, Ab10, each with a ring of fine hooks (Fig. 16.1.215); larvae mining aquatic vegetation and/or often shifting to a vegetative case later in development in still water, or living under sheet of silk on rocks in swift water ..... Lepidoptera
11′	Abdomen without ventral prolegs on Ab3 to Ab6 12
12(11)	Body caterpillar-like (Figs. 16.1.171 and 175); sometimes housed in organic or inorganic cases (Figs. 16.1.178, 181 and 189); antennae relatively short, inconspicuous, of a single article (Figs. 16.1.180 and 182) ..... **Trichoptera [p. 617]**
12′	Body not caterpillar-like; not housed in cases; antennae elongate, with three or more segments 13
13(12)	Long lateral filaments absent (Figs. 16.1.139, 141 and 144) ..... **Coleoptera** (in part) **[p. 601]**
13′	Long lateral filaments present (Figs. 16.1.105, 106, 142 and 143) 14
14(13)	Tarsus single-clawed *or* tarsi two-clawed and abdomen terminating in two slender filaments (Fig. 16.1.164) *or* tarsi two-clawed with a single median proleg terminating in four hooks (Fig. 16.1.143) ..... **Coleoptera** (in part) **[p. 601]**
14′	Tarsus two-clawed; abdomen terminating in a single slender filament (Fig. 16.1.105) or in two prolegs, each with two hooks (Figs. 16.1.106) ..... **Megaloptera [p. 599]**

Crustacea: Hexapoda: Ephemeroptera: Families

Barber-James et al. (2008) provide an estimate of the global diversity of mayflies with numbers of species and genera in all geographic realms, including the Palaearctic. This is an important resource for understanding global diversity of mayflies. Great strides have been made in synthesis of the European mayfly fauna, especially the massive work of Bauernfeind & Soldán (2012). Any serious student of mayflies working in the western Palaearctic must consult this resource. The work of Hong (1994), a key to the larval mayflies of China, is but a start on the work needed in that area and seriously out of date. Many recent species descriptions, revisions, and checklists covering the region have recently been published. Much more such work is needed, especially in China.

This key is modified from DeWalt & Resh (2016), Bauernfeind & Soldán (2012), and Waltz & Burian (2008).

1	Mandibles with large, anteriorly projecting tusks (Fig. 16.1.13); abdominal segments 2 to 7 with gills forked, margins fringed (Fig. 16.1.14) and projecting laterally or dorsally over abdomen 2
1′	Mandibles usually lacking large tusks; fringed gills absent or projecting ventrolaterally 6
2(1)	Gills projecting laterally; protibiae slender, subcylindrical (Fig. 16.1.15) 3
2′	Gills held dorsally; protibiae fossorial (Fig. 16.1.16) 4
3(2)	Mandibular tusks >2x length of head with many long setae (Fig. 16.1.17) ..... Euthyplociidae
3′	Mandibular tusks without many long setae ..... Potamanthidae
4(2)	Apex of metatibiae rounded (Fig. 16.1.18) 5
4′	Apex of metatibiae forming an acute point ventrally (Fig. 16.1.19); mandibular tusks curved upward or outward apically ..... Ephemeridae
5(4)	Mandibular tusk cross-section somewhat rounded, length curved inward and downward apically, crenulations on dorsal and lateral surfaces ..... Polymitarcyidae
5′	Mandibular tusks flattened, curved inward, then laterally, crenulation restricted to lateral edges of tusk ..... Palingeniidae

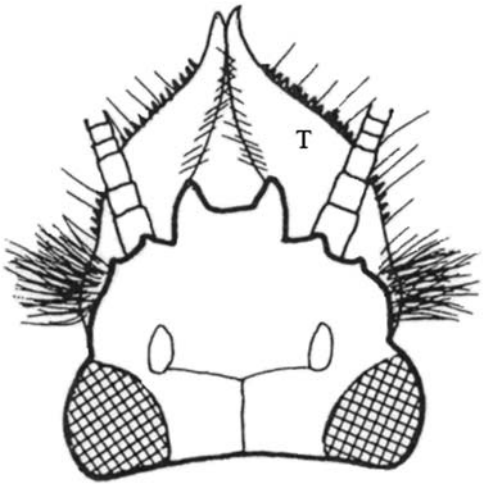


FIGURE 16.1.13 Ephemeridae, *Ephemera* head with mandibular tusks (dorsal).

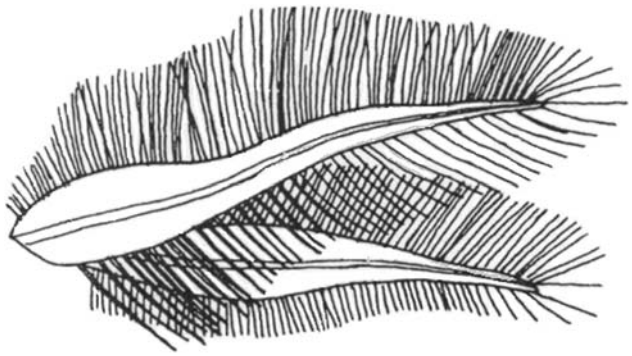


FIGURE 16.1.14 Ephemeridae, *Ephemera* forked gills (dorsal).

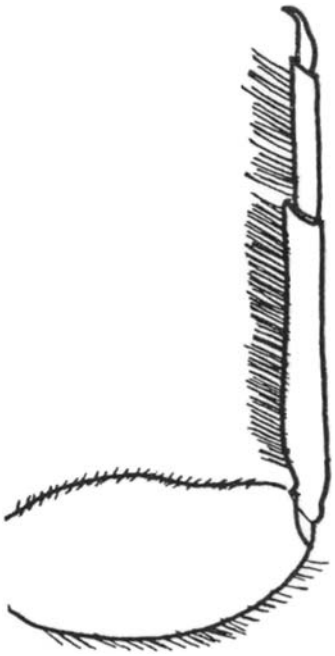


FIGURE 16.1.15 Potamanthidae, prothoracic leg (dorsal).



FIGURE 16.1.16 Ephemeridae, prothoracic leg (dorsal).



FIGURE 16.1.18 Polymitarcyidae, metathoracic leg (dorsal).

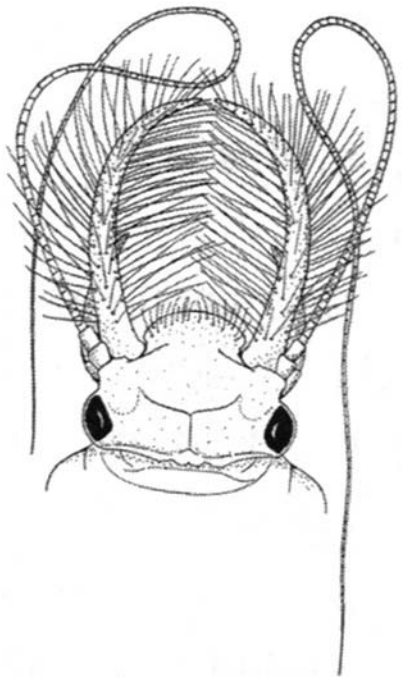


FIGURE 16.1.17 Euthyplociidae, head (dorsal). *Modified from Waltz & Burian (2008).*

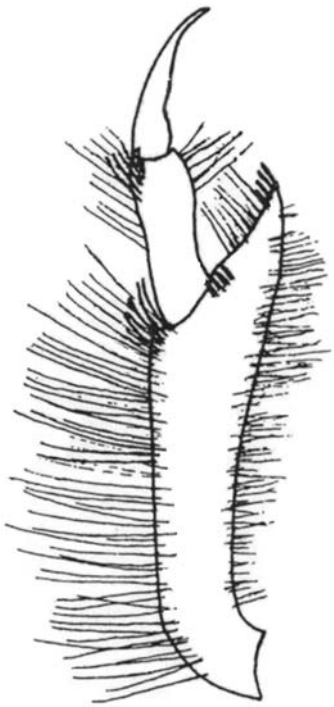


FIGURE 16.1.19 Ephemeridae, metathoracic leg.

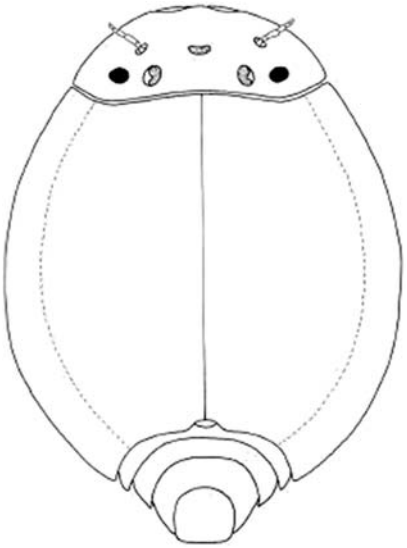


FIGURE 16.1.20 Prosopistomatidae, *Prosopistoma* habitus (dorsal). *Modified from Bojková & Soldán (2015).*

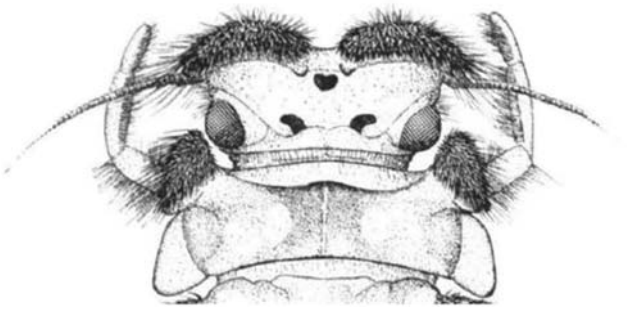


FIGURE 16.1.21 Behningiidae, *Behningia* head and pronotum (dorsal).

6(1)	Mesonotum not modified into a carapace, gills exposed 7
6′	Mesonotum modified into a carapace-like structure that completely covers all legs and Ab1−6 (Fig. 16.1.20) ..... Prosopistomatidae, one genus: *Prosopistoma* [Widespread]
7(6)	Head and pronotum without pads of long, dark setae; gills not fringed and projecting ventrolaterally 8
7′	Head and pronotum with pads of long, dark setae on each side (Fig. 16.1.21); fringed gills projecting ventrolaterally ..... Behningiidae [Poland, Romania, Russia]
8(7)	Gills on abdominal segment 2 operculate or semioperculate, covering or partially covering gills on succeeding segments (Figs. 16.1.22 and 23) 9
8′	Gills on abdominal segment 2 similar to those on succeeding segments (Fig. 16.1.24) or absent (Fig. 16.1.25); operculate gills may be present, but only on segments 3 or 4 10
9(8)	Operculate gills fused medially (Fig. 16.1.22) ..... Neoephemeridae [Europe, China]
9′	Operculate gills not fused medially, but may overlap (Fig. 16.1.23) ..... Caenidae
10(8)	Dorsum with Ab1−7 or Ab2−7 with gills (Fig. 16.1.24) 11
10′	Gills on Ab1−3 often missing, those on segment 3 or 4 may be operculate, covering succeeding gills (Fig. 16.1.25); head, thorax, and/or abdomen often have paired, median tubercles (related families Teloganodidae and Vietnamellidae are present just south of the Palaearctic Region) ..... Ephemerellidae
11(10)	Head and body not dorsoventrally flattened; eyes, and usually also antennae, along lateral margin of head (Fig. 16.1.27) 12
11′	Head flattened dorsoventrally with eyes and antennae dorsal (Fig. 16.1.26); gills a single lamella, some genera bearing gills with a ventral fibrilliform tuft ..... Heptageniidae
12(11)	Maxillary palp distal palpal segment short, usually not visible in dorsal view 13
12′	Maxillary palp distal segments setose and extending back over thorax and visible in dorsal view (Fig. 16.1.28) ..... Arthropleidae, one species: *Arthroplea congener* Bengtsson, 1909 [Europe to western Siberia]
13(12)	Protarsal claws much shorter than tibiae and those on other tarsi (Figs. 16.1.29); meso- and metatarsal claws long and slender, about as long as tibiae (Fig. 16.1.30) 14
13′	All tarsal claws similar in structure and length 15
14(13)	Protarsal claws bifid, procoxae without a spinose pad (Fig. 16.1.29) ..... Metretopodidae [northern Palaearctic]

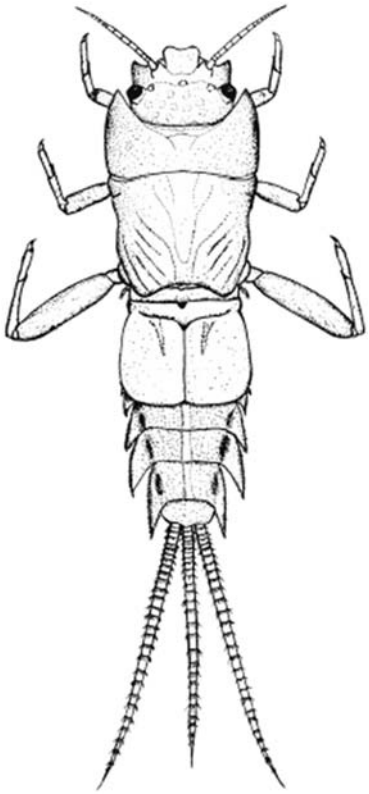


FIGURE 16.1.22 Neoephemeridae, *Neoephemera projecta* Zhou & Zheng, operculate gill (OG) (dorsal). *Modified from Zhou & Zheng (2001).*

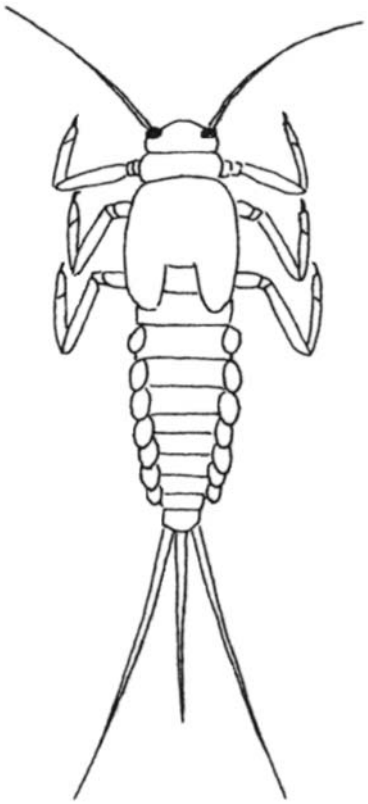


FIGURE 16.1.24 Baetidae habitus (dorsal).

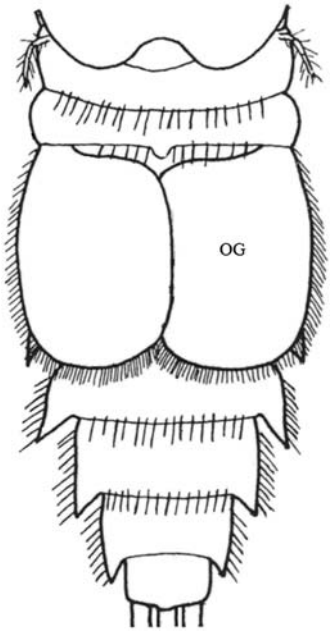


FIGURE 16.1.23 Caenidae, *Caenis*, operculate gill (OG) (dorsal).

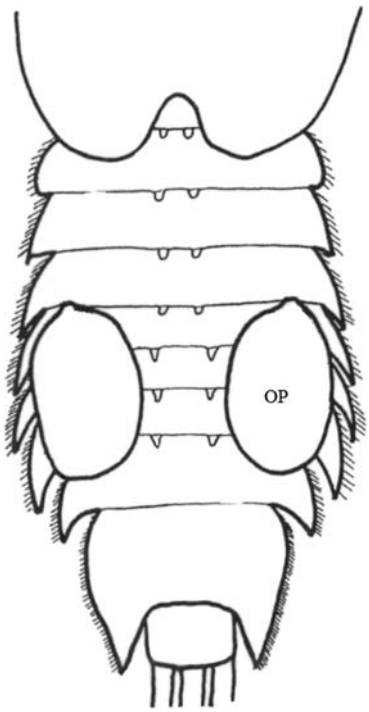


FIGURE 16.1.25 Ephemerellidae, operculate gill (OG) (dorsal).

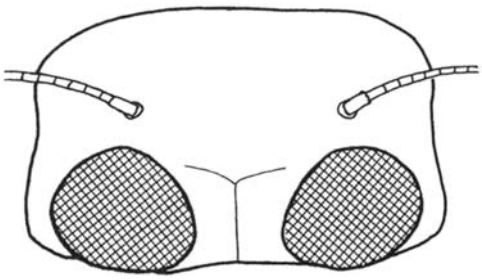


FIGURE 16.1.26 Heptageniidae, head (dorsal).

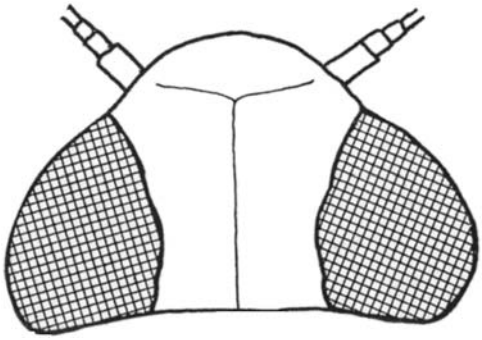


FIGURE 16.1.27 Siphlonuridae, head (dorsal).

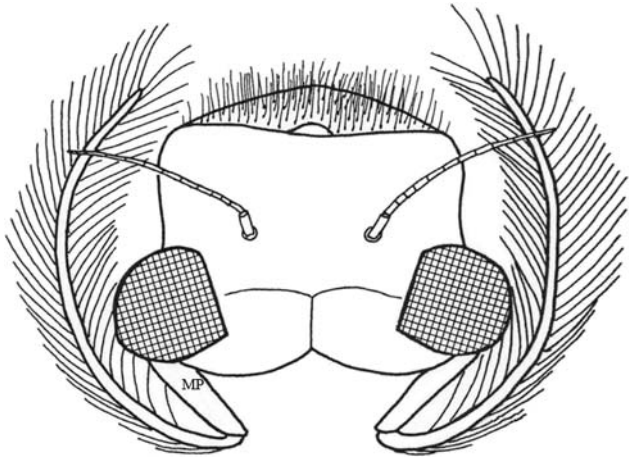


FIGURE 16.1.28 Arthropleidae, *Arthroplea* maxillary palp (MP) (dorsal).

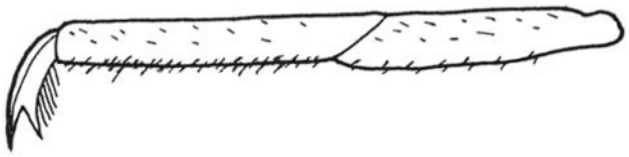


FIGURE 16.1.29 Metretopodidae, protarsus and tibia.



FIGURE 16.1.30 Ametropodidae, *Ametropus*, pro- and mesothoracic legs. *Modified from Waltz & Burian (2008).*

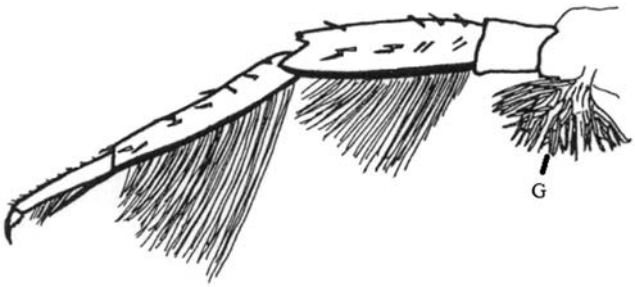


FIGURE 16.1.31 Isonychiidae, *Isonychia* prothoracic leg showing gills (G) (dorsal).

14′	Protarsal claws simple with long, slender denticles, procoxae with a spinose pad. (Fig. 16.1.30) ..... Ametropodidae, one species: *Ametropus fragilis* Albarda, 1878 [Europe to Siberia and Urals]
15(13)	Prothoracic femora and tibiae with dense, double row of long setae along inner surface (Fig. 16.1.31) 16
15′	Prothoracic legs without dense row of setae along inner surface 17
16(15)	Ab1 gills dorsolateral and similar to other gills, their ventral gill tufts shorter than gill plate; tufts of gills present at base of maxillae and forecoxae (Fig. 16.1.31) ..... Isonychiidae, one genus: *Isonychia*

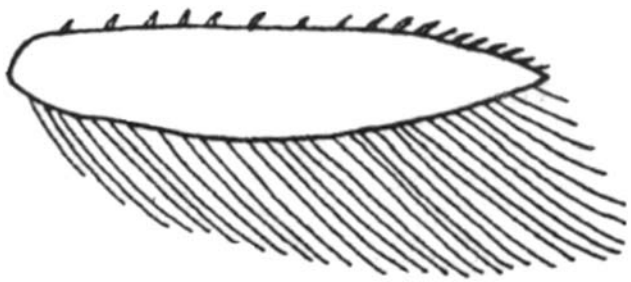


FIGURE 16.1.32 Oligoneuriidae, mid-abdominal gill (dorsal).



FIGURE 16.1.33 Siphlonuridae, *Siphlonurus* bilamillate abdominal gills (dorsal).



FIGURE 16.1.34 Leptophlebiidae, *Paraleptophlebia* forked gills (dorsal).

16′	Ab1 gills ventral, gills on abdominal segments 2–7 shorter than segments, either lanceolate with a posterior fringe (Fig. 16.1.32), or rounded and plate like; no gill tuft at base of procoxae ..... Oligoneuriidae
17(15)	Gills single (Fig. 16.1.24) or double lamellae (Figs. 16.1.33) 18
17′	Gills forked (Fig. 16.1.34), or bilamellate and terminating in a point (Fig. 16.1.35), or terminating in filaments (Fig. 16.1.36) .... Leptophlebiidae
18(17)	Tibiae and tarsi not bowed, claws usually not long and slender 19
18′	Metatibiae and tarsi bowed, claws long (Fig. 16.1.37); terga and sterna with sharp projections .... Acanthametropodidae, one species: *Acanthametropus nikolskyi* Tshernova, 1948 [Amur River, Russia]
19(18)	Abdominal segments 8 and 9 produced posterolaterally into distinct, flattened spines (Fig. 16.1.38); if spines are weak, antennae more than twice width of head 20
19′	Abdominal segments 8 and 9 without such spines; if weak spines are present, antennal length less than twice width of head .... Baetidae
20(19)	Maxillae with crown of pectinate spines (Fig. 16.1.39); gills single, with sclerotized band on ventral margin, little or no tracheation present ..... Ameletidae
20′	Maxillae without a crown of pectinate spines; gills single or double with well-developed tracheation (Fig. 16.1.33) ..... Siphlonuridae

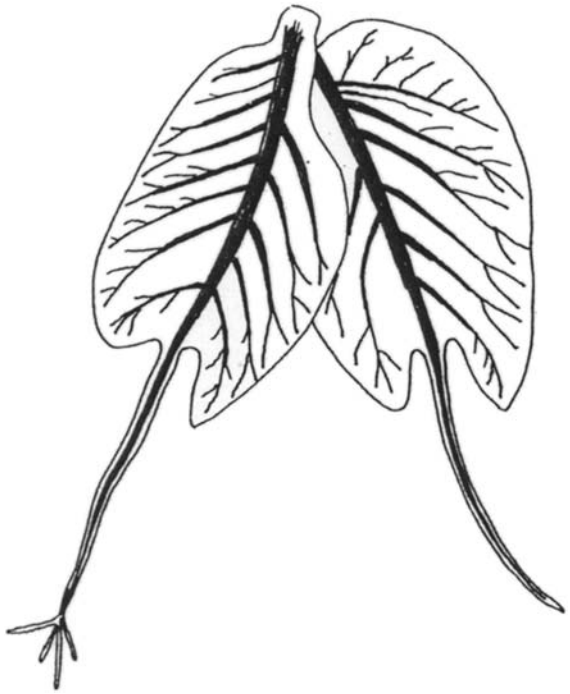


FIGURE 16.1.35 Leptophlebiidae, *Leptophlebia* plate-like/lanceolate gills Ab3.

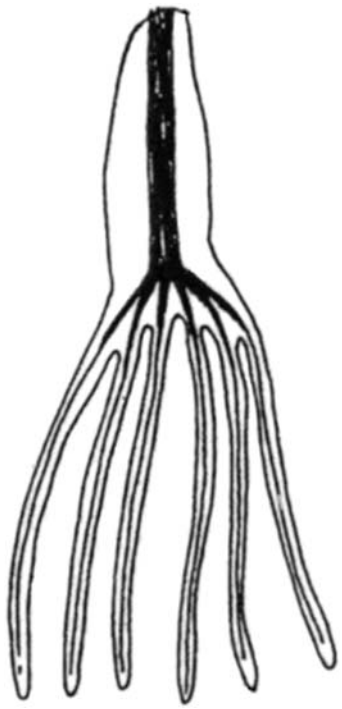


FIGURE 16.1.36 Leptophlebiidae, *Habrophlebia* gill filaments of Ab3.

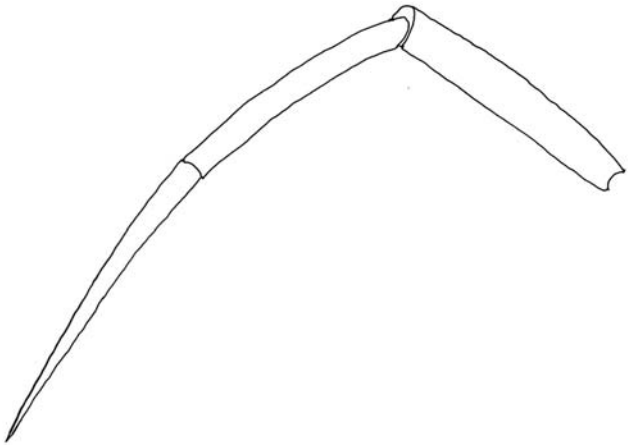


FIGURE 16.1.37 Acanthametropidae, *Acanthametropus* metatarsal leg.



FIGURE 16.1.38 Ameletidae, terminal abdominal segments of *Ameletus*, dorsal. *Modified from Zloty (1997).*



FIGURE 16.1.39 Ameletidae, *Ameletus* pectinate comb (arrow) setae on maxilla. *Modified from Tiunova (2013).*

Hexapoda: Insecta: Odonata: Families

This key covers families of Odonata as far south as Hainan Province, China. Key modified from DeWalt & Resh (2016), Norling & Sahlén (1997), and Kriska (2014). We have adopted the higher classification of Blanke et al. (2013) and others who treat the Anisozygoptera plus the dragonflies (Anisoptera) as the suborder Epiprocta. All the damselflies are still contained within the monophyletic suborder Zygoptera. The once subfamily Chlorogomphinae of the Cordulegastridae is presented as the family Chlorogomphidae (Dumont et al. 2009), and characters presented for its separation are from Zhang & Tong (2013).

Dijstra et al. (2014) conducted a revision of the Zygoptera based on mitochondrial (16S, COI) and nuclear (28S) data of 59% of the 310 recognized genera and all but one of the suspected families. They confirmed the monophyly of many families, but also discovering paraphyletic or polyphyletic families that necessitated the transfer of genera between families. Their paper presents a new classification of the order. The key for Zygoptera reflects some of these classificatory changes.

1	Abdomen cylindrical, narrow, with three caudal gills (Fig. 16.1.40)	suborder Zygoptera 2
1′	Abdomen broad, lacking exposed caudal gills (Figs. 16.1.41 and 42)	suborder Epiprocta 9
2(1)	First antennal segment as long as remaining segments combined (Fig. 16.1.43); prementum deeply cleft (Fig. 16.1.44)	 3
2′	First antennal segment shorter than others; prementum with at most a very small median cleft	 4
3(2)	Median caudal gill strongly reduced (Fig. 16.1.45)	Chlorocyphidae
3′	Median caudal gill elongate, lamellate (Fig. 16.1.40)	Calopterygidae
4(2)	Finger-like gills present on abdominal segments 2–8 (Fig. 16.1.46)	Euphaeidae
4′	Finger-like gills absent from abdominal segments	 5
5(4)	Ventral, retractable, paired gill tufts at base of Ab10 (Fig. 16.1.47)	Pseudolestidae
5′	Larvae without ventral, retractable, paired, gill tufts on Ab10	 6
6(5)	Caudal gills held in vertical plane	 7
6′	Caudal gills all held in horizontal plane (as in Fig. 16.1.48)	Argiolestidae, one genus: *Podolestes* [Hainan, China (extralimital)]
7(6)	Prementum base broad (Fig. 16.1.50)	 8
7′	Prementum base greatly narrowed and elongate (Fig. 16.1.49)	Lestidae
8(7)	Prothorax with distinct dorsal bulges (Fig. 16.1.51); lateral caudal gills with long, acuminate, hairy apex (Fig. 16.1.52).	..... Platycnemididae
8′	Prothorax without bulges (Fig. 16.1.53); lateral caudal gills tip may be pointed, but not acuminate and hairy; gills often divided transversally at midlength (Fig. 16.1.54)	Coenagrionidae
9(1)	Antenna three, four, six, or seven segmented (Figs. 16.1.57–59); abdomen without files	 10
9′	Antennae five segmented (Fig. 16.1.55); lateral abdominal files for sound production present (Fig. 16.1.56)	..... Epiophlebiidae, one genus: *Epiophlebia* [China, Japan]
10(9)	Prementum flat or nearly so, without dorsal setae (Fig. 16.1.60); palpal lobes also flat and usually without stout setae	 11
10′	Prementum rounded, spoon-shaped and covering face (Fig. 16.1.61); palpal lobes rounded	 13
11(10)	Antennae with six or seven articles; pro- and mesothoracic tarsi 3-articulate	 12
11′	Antennae 4-articulate (4th may be minute), segment 3 often longer than other segments combined (Fig. 16.1.58); pro- and mesothoracic tarsi 2-articulate	..... Gomphidae
12(11)	Antennal articles slender, not setose (Fig. 16.1.57)	Aeshnidae
12′	Antennal articles short, thick, and setose (Fig. 16.1.59)	Petaluridae, one species: *Tanypteryx pryeri* Kennedy, 1889 [Japan]
13(10)	Palpal lobe with distal margins having large, irregular teeth (Fig. 16.1.62)	 14
13′	Palpal lobes with distal margins having small, even crenulations (Figs. 16.1.64) or nearly straight (Fig. 16.1.65)	 15
14(13)	Wingpads divergent (Fig. 16.1.66); body surface finely granulate with contrasting pigmentation, especially on abdomen (may initially be mistaken for Gomphidae, but with seven segmented filiform antennae as in Fig. 16.1.57)	..... Chlorogomphidae
14′	Wingpads not divergent (Fig. 16.1.67); body surface not granulate or contrasting in pigmentation	Cordulegastridae
15(13)	Head without a prominent frontal process; legs shorter, apex of metafemora usually not reaching apex of abdominal segment 8; metasternum without a median tubercle	 16
15′	Head with a prominent, almost erect, thick frontal process between bases of antennae (Fig. 16.1.68); legs very long, apex of each metafemur reaching to or beyond apex of abdominal segment 8; metasternum with broad, median tubercle	Macromiidae

16(15) Palpal lobe crenulations large, at least 1/4 as long as wide (Figs. 16.1.63) 17

16′ Palpal lobe crenulations very shallow, 1/6 to <1/10 as long as wide (Fig. 16.1.65) or separated by minute notches bearing setae (Fig. 16.1.64) ..... Libellulidae (in part)

17(16) Abdominal segment 8 with lateral spines as long or longer than mid-dorsal length of segment 9 (Fig. 16.1.69); ventral surface of prementum lacking median groove extending from base to halfway up ligula (Fig. 16.1.70) ..... Libellulidae (in part)

17′ Abdominal segment 8 with lateral spines shorter than mid-dorsal length of segment 9; ventral surface of prementum having median groove extending from base to halfway up ligula (Fig. 16.1.71); rounded projections on distal margin of palpal lobe separated by deep notches, projections up to twice as long as wide (Fig. 16.1.63) ..... Corduliidae

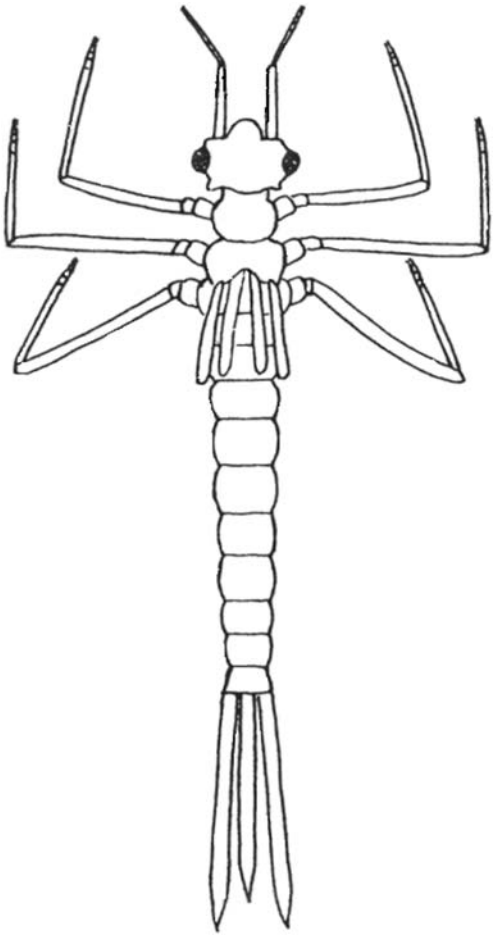


FIGURE 16.1.40 Calopterygidae, Calopteryx larva (dorsal).

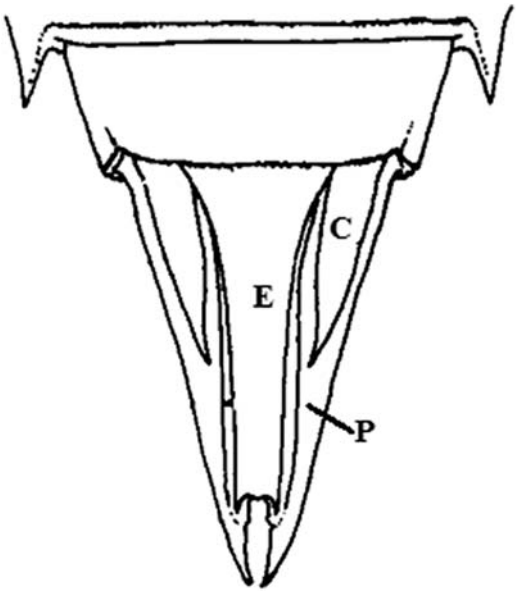


FIGURE 16.1.41 Aeshnidae, larval terminalia, (dorsal). C=cercus, E=epiproct, and P=paraproct.

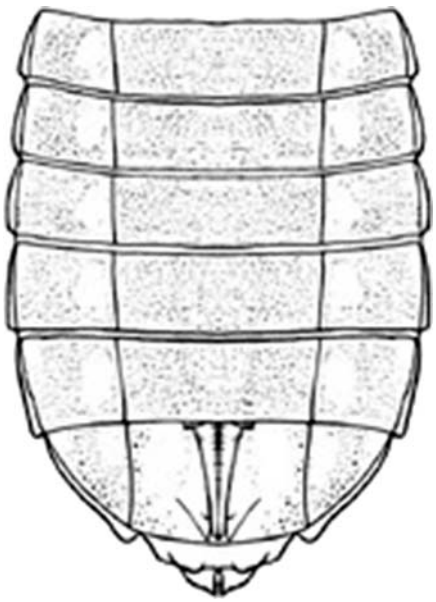


FIGURE 16.1.42 Epiophlebiidae, *Epiphlebia* larval abdomen (ventral). *Modified from Carle (2012).*

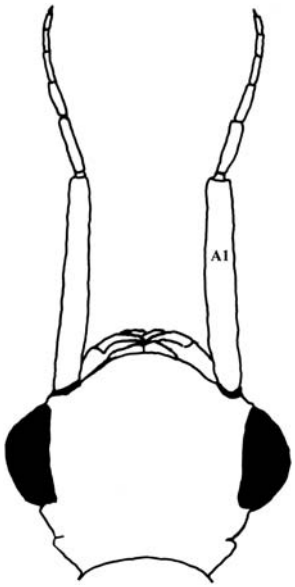


FIGURE 16.1.43 Calopterygidae, *Calopteryx* head (dorsal). A1=first antennal segment.

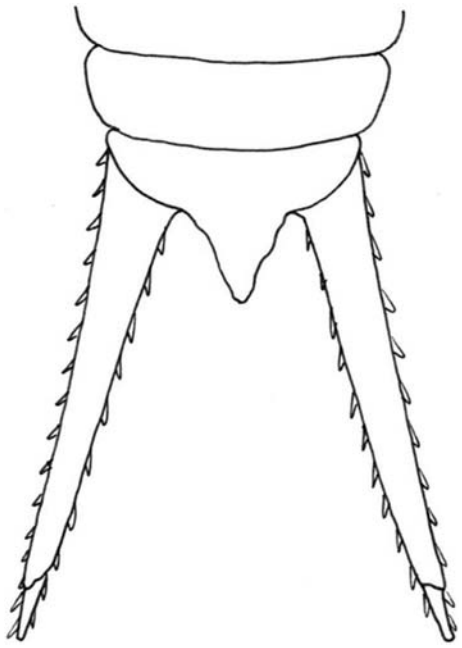


FIGURE 16.1.45 Chlorocyphidae, caudal gills (dorsal).

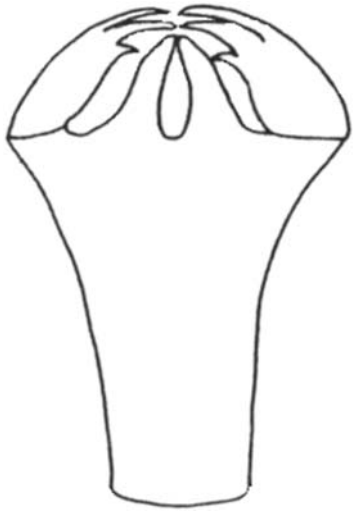


FIGURE 16.1.44 Calopterygidae, cleft prementum of *Calopteryx* (dorsal view). A1=antennal segment 1.

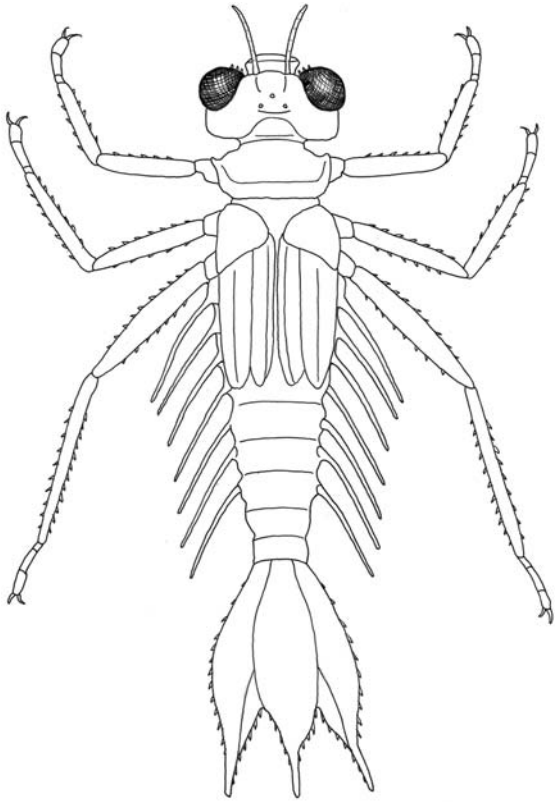


FIGURE 16.1.46 Euphaeidae, *Euphaea impar* Sélys nymphal habitus (dorsal). *Modified from Lok & Orr (2009).*

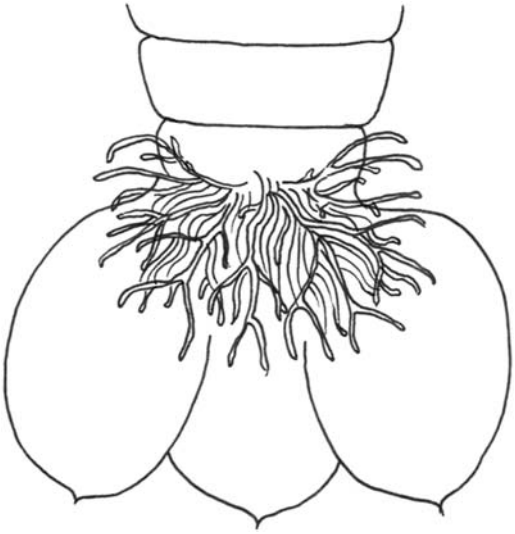


FIGURE 16.1.47 Pseudolestidae, *Pseudolestes mirabilis* Kirby, larval abdominal tip with Ab10 caudal gills (ventral). *Modified from Yu & Bu (2014).*

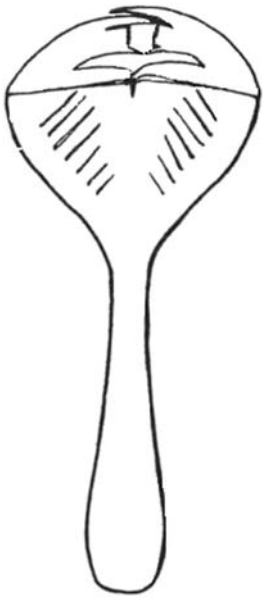


FIGURE 16.1.49 Lestidae, prementum and labial palps (dorsal).



FIGURE 16.1.48 Argiolestidae, *Metagrion pectitum* (Lieftinck) habitus (dorsal). *Modified from Lieftinck (1956).*

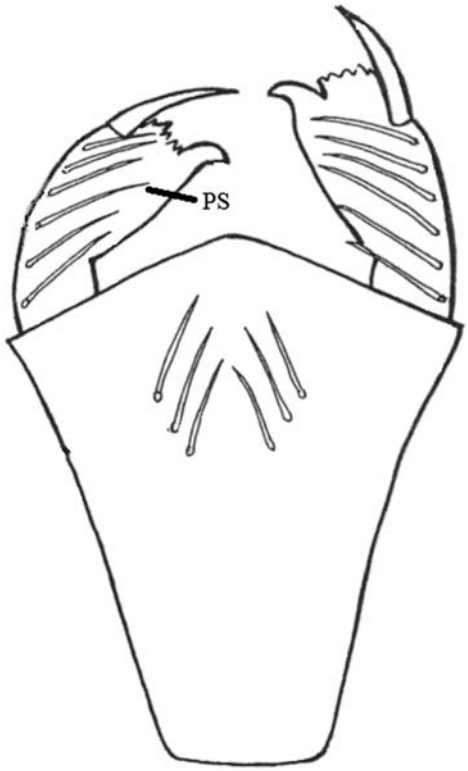


FIGURE 16.1.50 Coenagrionidae, prementum (dorsal). PS=palpal setae.

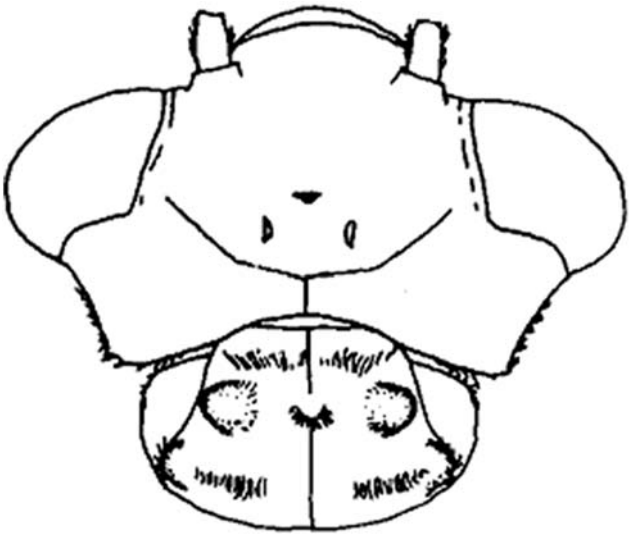


FIGURE 16.1.51 Platycnemididae, *Platycnemus* pronotal tubercles (dorsal). *Modified from Norling & Sahlén (1997).*

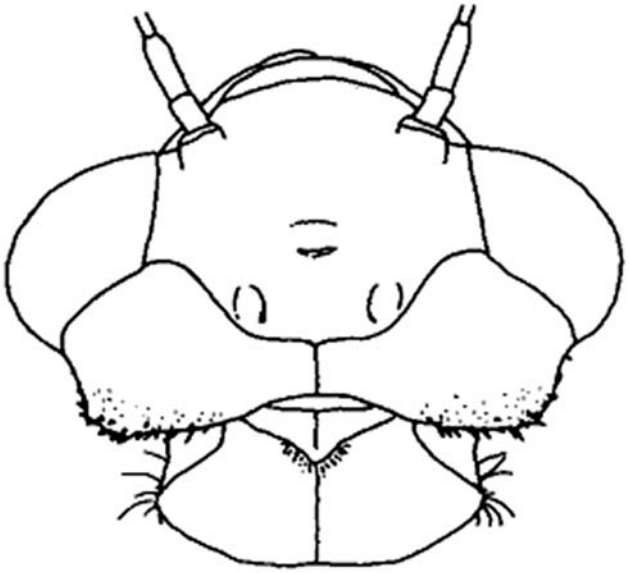


FIGURE 16.1.53 Coenagrionidae, *Pyrrhosoma* head and pronotum (dorsal). *Modified from Norling & Sahlén (1997).*



FIGURE 16.1.52 Platycnemididae, *Platycnemus* caudal gill (lateral). *Modified from Norling & Sahlén (1997).*



FIGURE 16.1.54 Coenagrionidae, *Pyrrhosoma* caudal gill (lateral). *Modified from Norling & Sahlén (1997).*

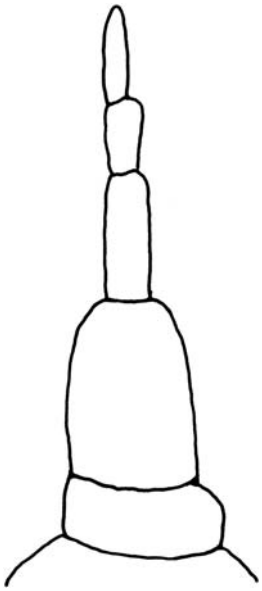


FIGURE 16.1.55 Epiophlebiidae, *Epioplebia* larval antenna. *Modified from Carle (2012).*

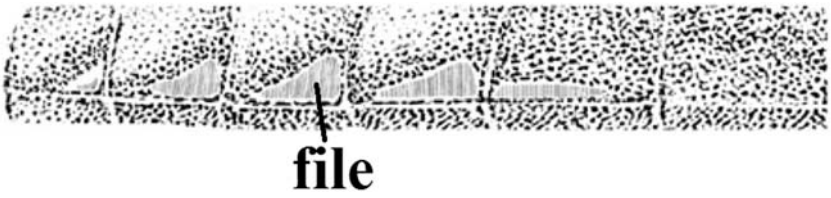


FIGURE 16.1.56 Epiophlebiidae, *Epiophlebia* larval abdomen with stridulatory surfaces (file), lateral. *Modified from Carle (2012).*

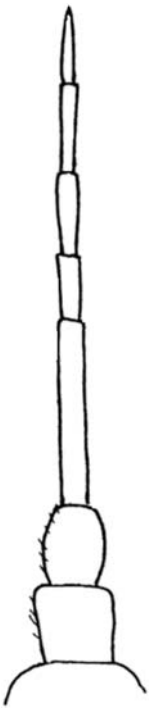


FIGURE 16.1.57 Aeshnidae antenna.



FIGURE 16.1.58 Gomphidae antenna.

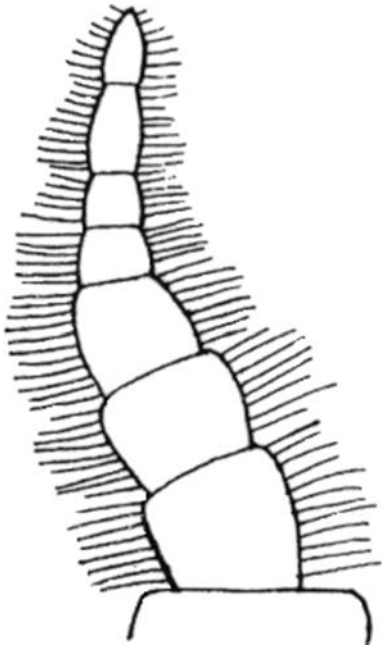


FIGURE 16.1.59 Petaluridae antenna.

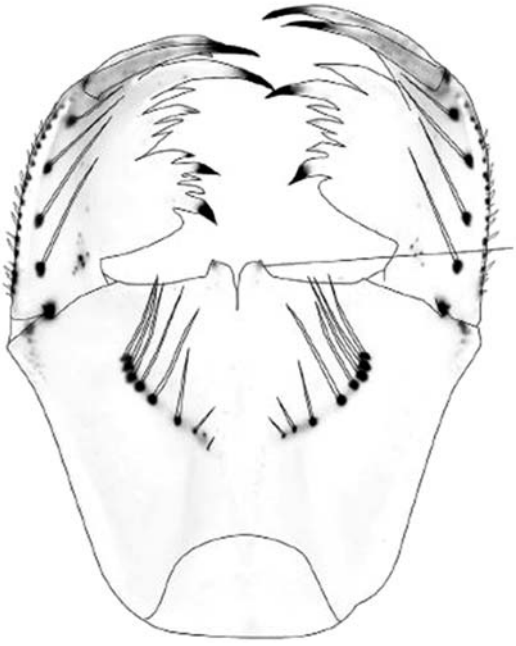


FIGURE 16.1.62 Chlorogophidae, *Chlorogomphus* prementum (dorsal). *Modified from Zhang & Tong (2013).*

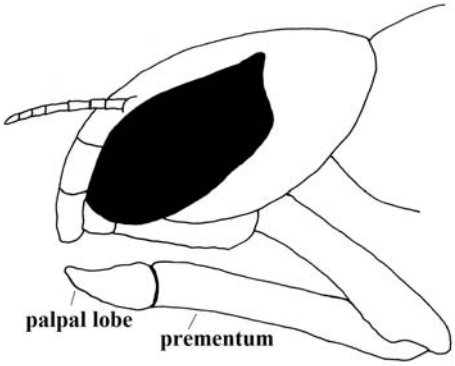


FIGURE 16.1.60 Aeshnidae, flat mentum (lateral). *Modified from Bouchard (2009).*

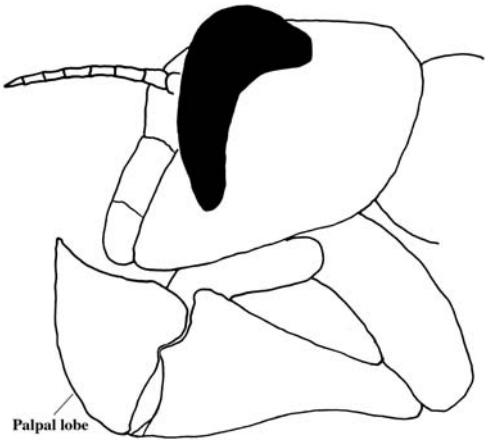


FIGURE 16.1.61 Libellulidae, scooped mentum (lateral). *Modified from Bouchard (2009).*



FIGURE 16.1.63 Corduliidae, labial palp (dorsal).



FIGURE 16.1.64 Libellulidae, labial palp (dorsal).



FIGURE 16.1.65 Libellulidae, labial palp (dorsal).



FIGURE 16.1.66 Chlorogophidae, *Chlorogomphus* habitus (dorsal). *Modified from Zhang & Tong (2013).*



FIGURE 16.1.67 Cordulegastridae, *Cordulegaster insignis* Schneider habitus (dorsal). *Modified from Holuša & Holušová (2012).*

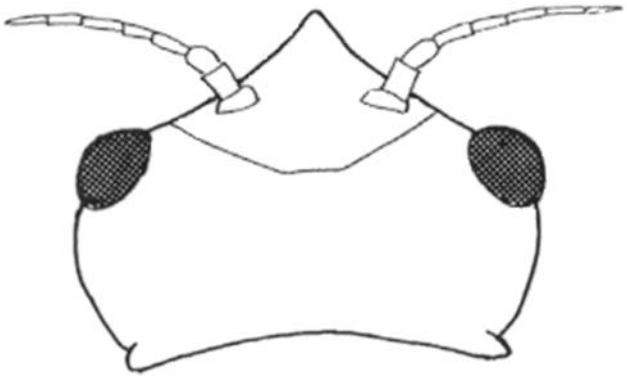


FIGURE 16.1.68 Macromiidae, *Macromia* head with frontal horn.

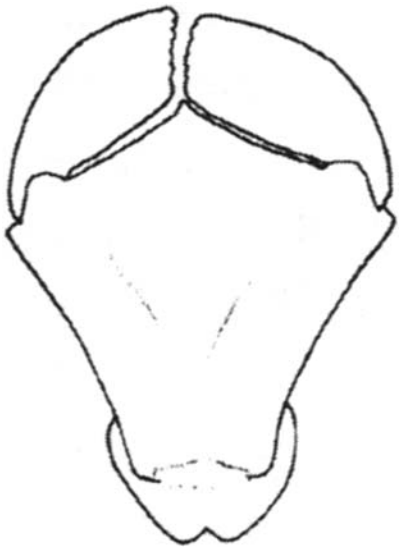


FIGURE 16.1.70 Libellulidae, *Pachydiplax* prementum (ventral).

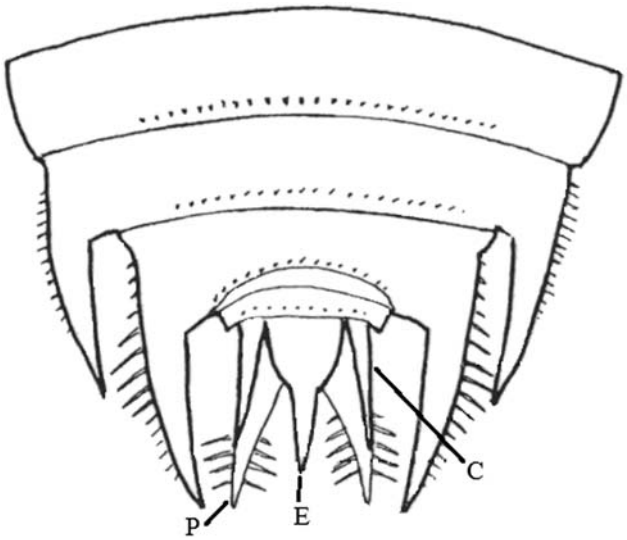


FIGURE 16.1.69 Libellulidae, *Pantala* abdominal segments 7–10 (dorsal view) showing epiproct (E), cerci (C), and paraprocts (P).

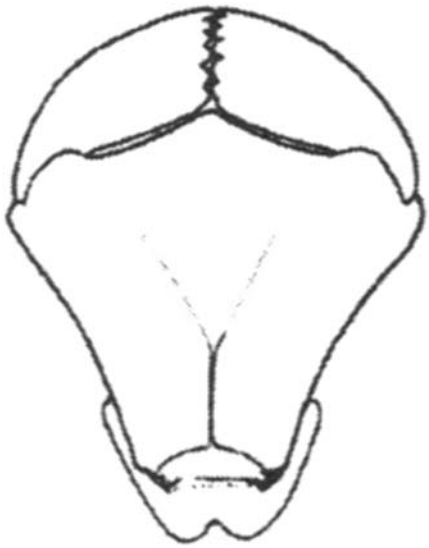


FIGURE 16.1.71 Corduliidae, *Epitheca* prementum (ventral).

Hexapoda: Insecta: Plecoptera: Families

This key is modified from Stewart & Stark 2002 with updates from Uchida and Isobe 1989, and Zwick 2000, and Zwick 2004.

Fochetti & Tierno de Figueroa (2008) summarized the diversity and distribution of stoneflies at the global level. Zwick (2004, 2006) provided a solid basis for identification of families in the western Palaearctic and at the global scale, respectively. Keys exist to species for larvae and adults of stoneflies in the western Palaearctic (Hynes 1977, Koese 2008, Brittain & Saltveit 1996, and others). A key to nymphs of China (Harper 1994) is also available. A wealth of primary literature describing new species, associating life stages, and providing checklists of species from the Palaearctic is available; much more is needed, especially in China. A wealth of basic biological information is available in the Zwick (2000) review and in Stewart & Stark (2002).

1	Gill tufts absent from thorax and Ab1−2, but may be present singly, paired, as tufts elsewhere on the body 2
1′	Gill tufts on thorax and Ab1 and Ab2 (Fig. 16.1.72) ..... Pteronarcyidae
2(1)	Body not roach-like, thorax not wider than head and abdomen 3
2′	Body roach-like, thorax far wider than head and abdomen (Fig. 16.1.73) ..... Peltoperlidae
3(2)	Apex of tibia with or without spur, without trifurcate setae 4
3′	Apex of tibia without spur, with trifurcate setae (Fig. 16.1.74) ..... Styloperlidae
4(3)	Numerous gill filaments not found between Ab9 and Ab10 5
4′	Numerous gill filaments restricted to between Ab9 and Ab10 (Fig. 16.1.75) ..... Scopuridae
5(4)	Apex of labial palps do not extend beyond paraglossae, glossae and paraglossae of about equal length (Fig. 16.1.76); mandibles and lacinia generally blunt, mandibles with wide mola area (Fig. 16.1.77), mouthparts for grinding and scraping of plant material 6
5′	Apex of labial palps reach well beyond paraglossae, paraglossae longer than glossae (Fig. 16.1.78); mandibles and lacinia sharply toothed for predation (Fig. 16.1.79) 9
6(5)	Tarsal segments 1 and 2 unequal, segment 1 longer than segment 2 (Fig. 16.1.81). 7
6′	Tarsal segments 1 and 2 of about same length (Fig. 16.1.80) ..... Taeniopterygidae
7(6)	Slender, often light-colored insects; extended hind legs do not reach tip of abdomen—long abdomen; wingpads in last few instars parallel to body axis (Fig. 16.1.83) (except *Capnioneura*, which has divergent wingpads) 8
7′	Small, but stout, dark insects; extended hind legs reach to tip of abdomen or beyond; wingpads in last few instars divergent from body axis (Fig. 16.1.82) ..... Nemouridae
8(7)	Mentum small, not covering base of maxillae (often light-colored, Fig. 16.1.84); metathoracic wingpads, if present, only as long as wide ..... Capniidae
8′	Mentum larger, covering bases of maxillae (Fig. 16.1.85); metathoracic wingpads usually longer than wide (Fig. 16.1.83) ... Leuctridae
9(5)	Tufts of gills absent, but some small, finger-like single gills may be present on either side of mentum or on thorax or abdomen 10
9′	Thorax (and sometimes at base of paraprocts) with tufts of finger-like gills (Figs. 16.1.1 and 86); habitus flat, legs flat and extended laterally with long setal fringes ..... Perlidae
10(9)	Dorsally, head and protruding bases of maxillae often as wide or wider than the prothorax (Fig. 16.1.87); terminal segment of maxillary palps only slightly smaller than penultimate segment and inserted symmetrically; wingpads often divergent, medial margins U-shaped; some genera have a digitiform gill on each side of the mentum (Fig. 16.1.88) or similarly on thorax (Fig. 16.1.89) ..... Perlodidae
10′	Dorsally, head and maxillae no wider than pronotum; terminal segment of maxillary palps much smaller than penultimate segment, peg-like, inserting asymmetrically (Fig. 16.1.90) (except for *Kathroperla* (Russian Far East) where it is larger and symmetrically placed); wingpads externally rounded (Fig. 16.1.91), the medial margins V-shaped; gills lacking ..... Chloroperlidae

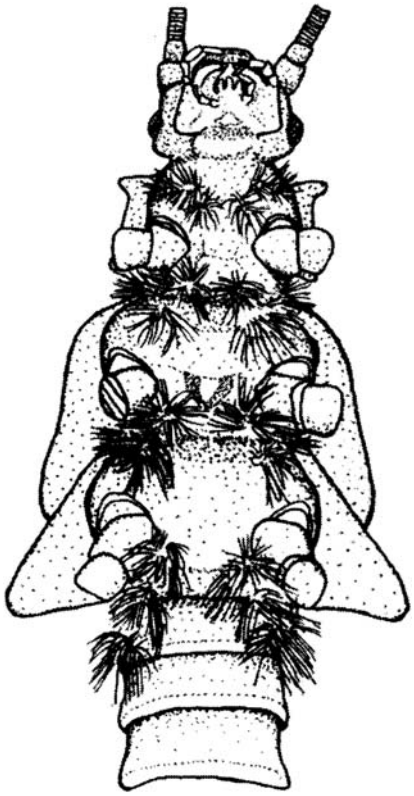


FIGURE 16.1.72 Pteronarcyidae, *Pteronarcys* thoracic and abdominal gills (ventral). *Modified from Stewart & Stark (2002).*

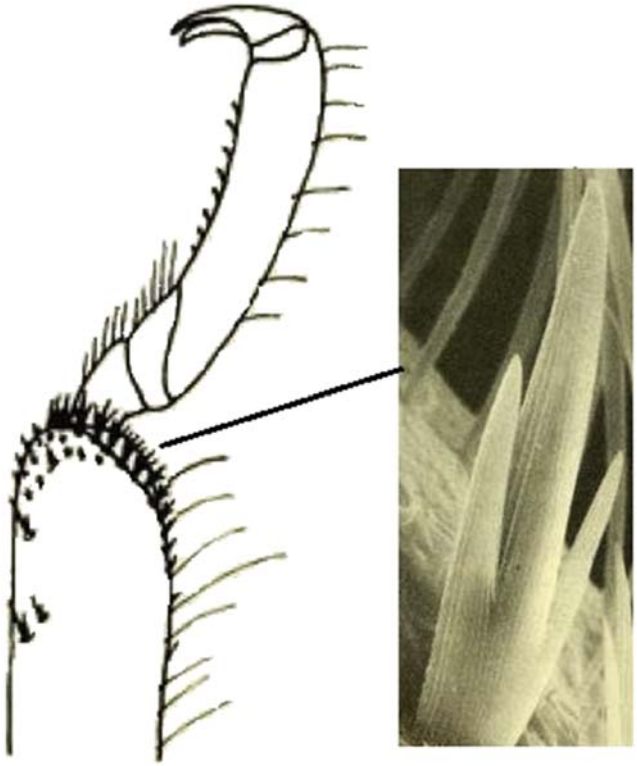


FIGURE 16.1.74 Styloperlidae, *Cerconychia livida* Klapálek tibial apex lacking large terminal spurs. Inset demonstrating trifurcate setae. *Modified from Uchida & Isobe (1989).*

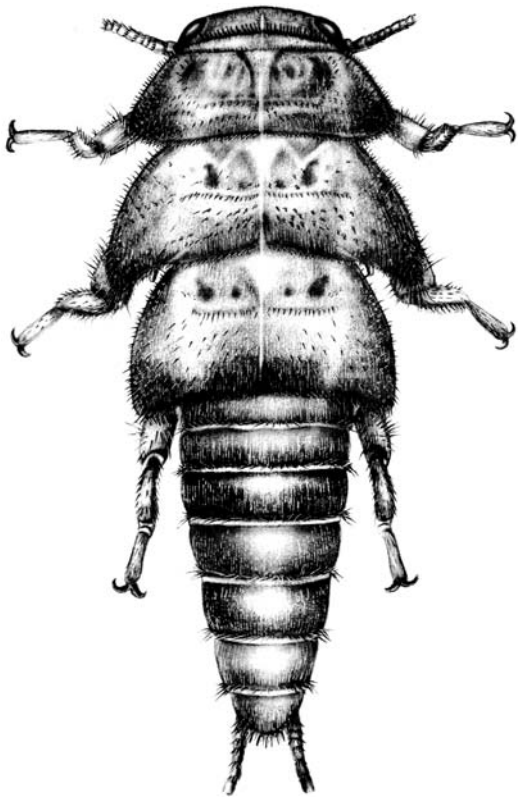


FIGURE 16.1.73 Peltoperlidae, *Yoraperla* habitus (dorsal). *Modified from Stewart & Stark (2002).*



FIGURE 16.1.75 Scopuridae, *Scopura longa* Uéno gills of intersegmental membrane between Ab9, 10 (lateral). Japan, Honshu Is., Aomori Pref., trib. Lake Towada, August 7, 1937, M. Kohno. INHS Plecoptera-15607.

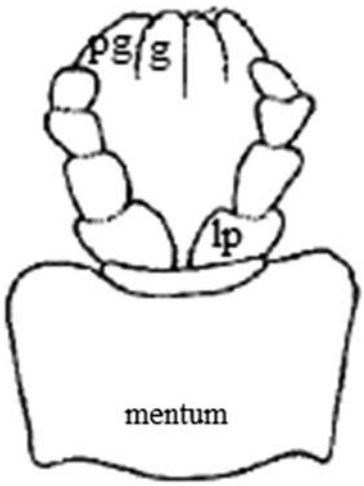


FIGURE 16.1.76 Nemouridae, labium (ventral). *Modified from Sivec & Yule (2004).*

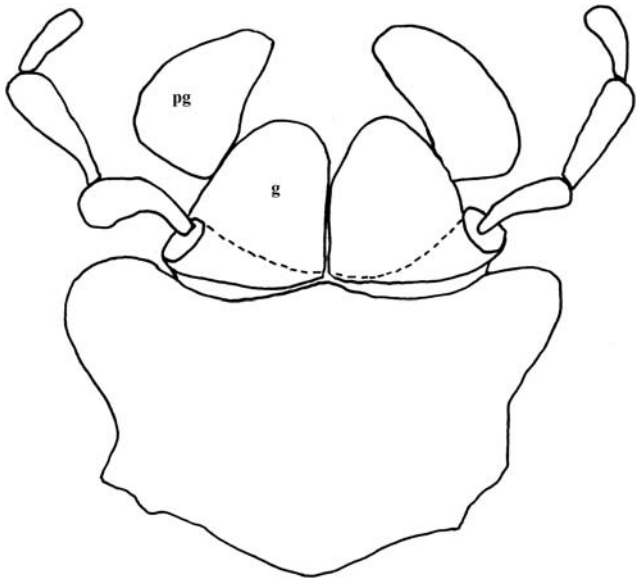


FIGURE 16.1.78 Perlidae, labium (ventral). *Modified from Sivec & Yule (2004).*

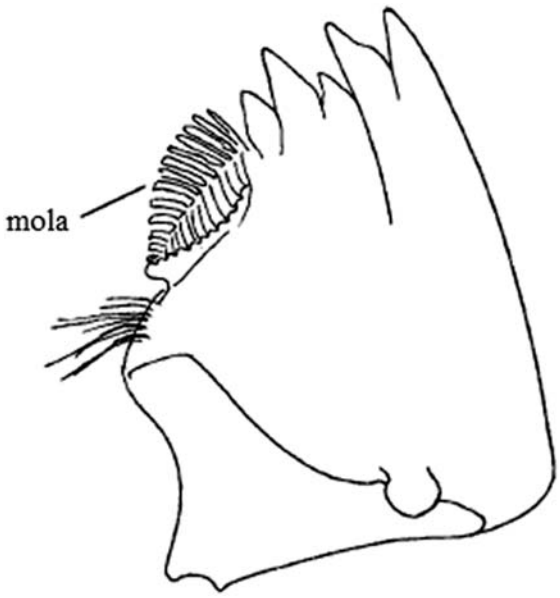


FIGURE 16.1.77 Nemouridae, *Nemoura* right mandible and flat mola (dorsal). *Modified from Zwick (2004).*



FIGURE 16.1.79 Perlodidae, mandible (dorsal). *Modified from Zwick (2004).*

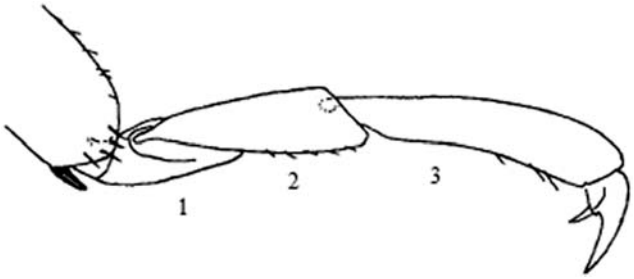


FIGURE 16.1.80 Taeniopterygidae, tarsus (lateral). *Modified from Zwick (2004).*

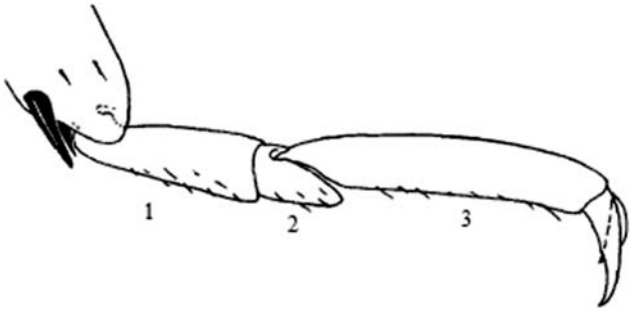


FIGURE 16.1.81 Leuctridae tarsus (lateral). *Modified from Zwick (2004).*

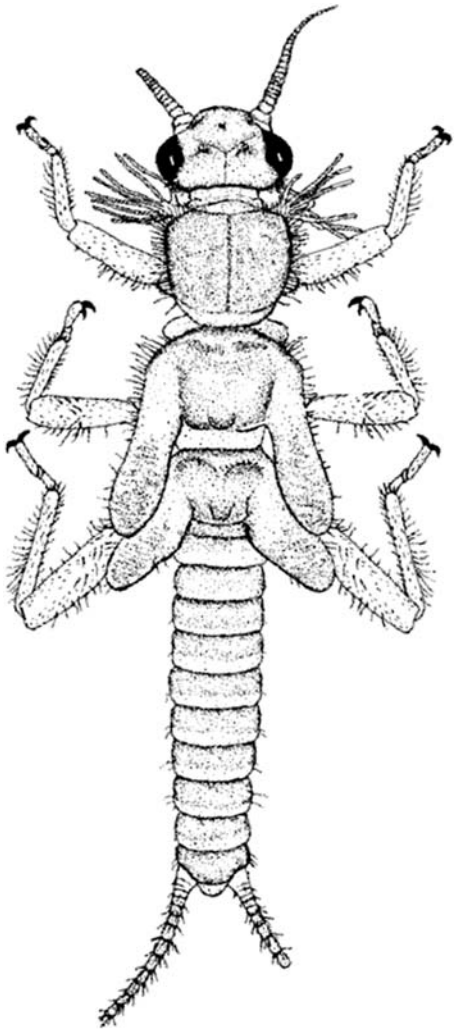


FIGURE 16.1.82 Nemouridae habitus (dorsal). *Modified from Sivec & Yule (2004).*

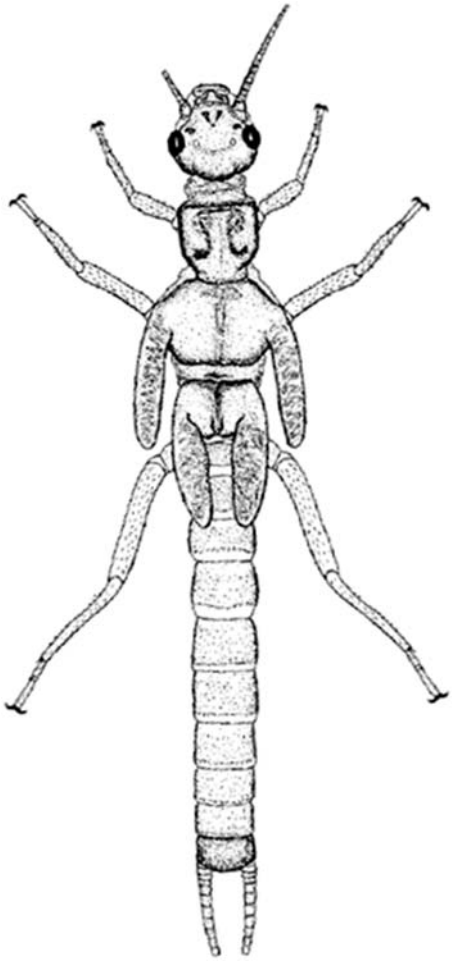


FIGURE 16.1.83 Leuctridae habitus (dorsal). *Modified from Sivec & Yule (2004).*

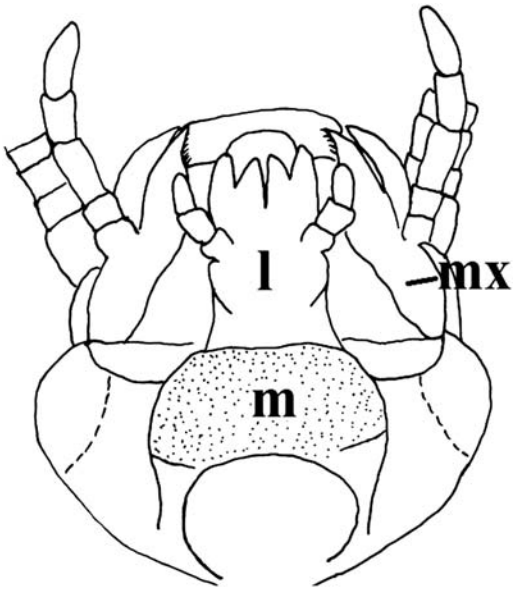


FIGURE 16.1.84 Capniidae, mentum (ventral). *Modified from Zwick (2004).*

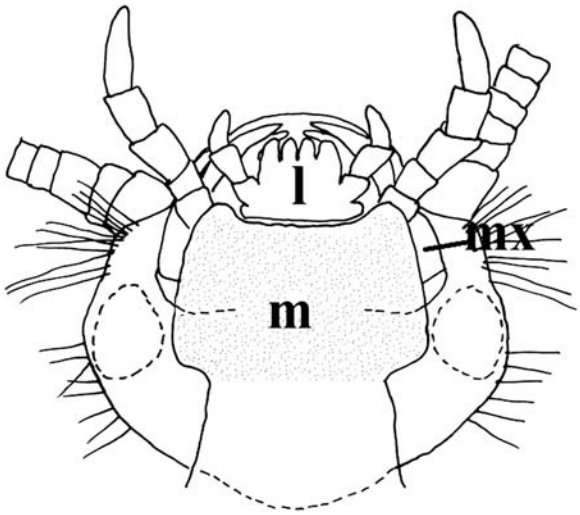


FIGURE 16.1.85 Leuctridae, mentum (ventral). *Modified from Zwick (2004).*

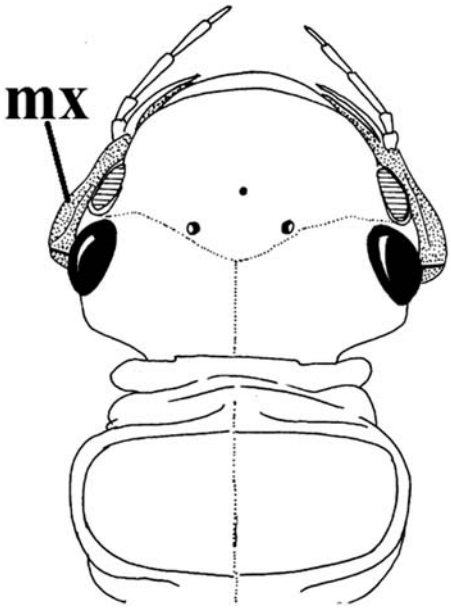


FIGURE 16.1.87 Perlodidae, head and prothorax (dorsal). Protruding bases of maxillae stippled. *Modified from Zwick (2004).*

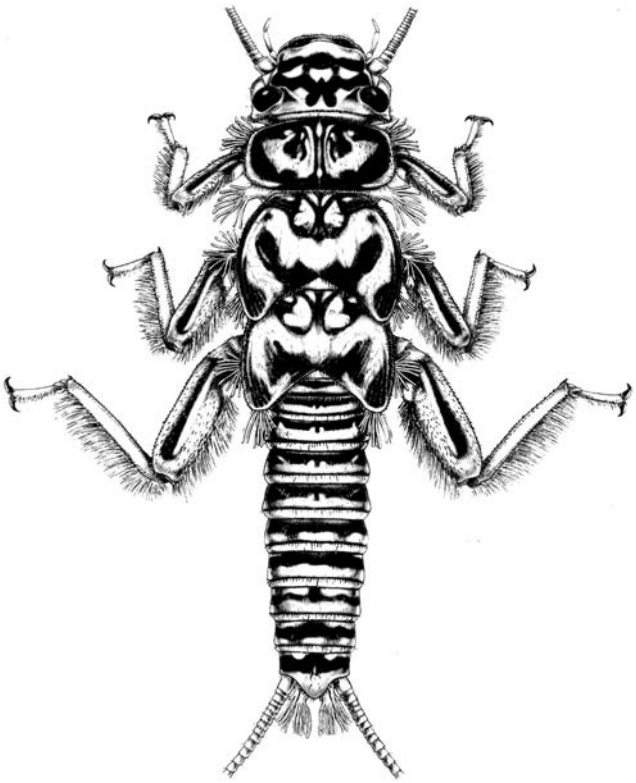


FIGURE 16.1.86 Perlidae, habitus showing thoracic gills (dorsal). *Modified from Stewart & Stark (2000).*

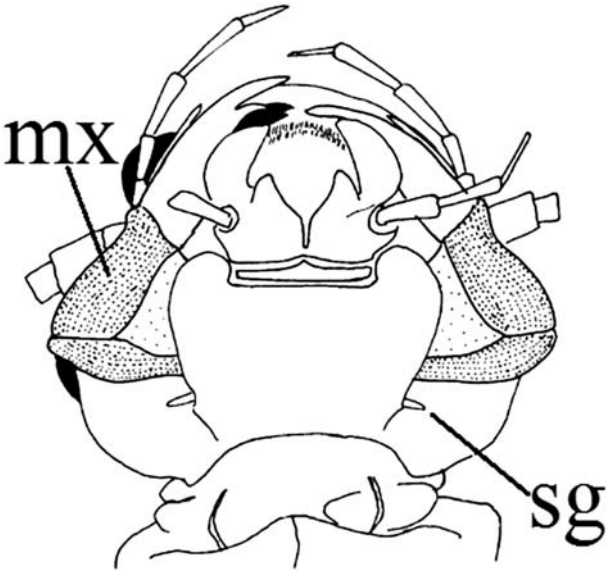


FIGURE 16.1.88 Perlodidae, head and prothorax (ventral). M=maxilla base, SG=submental gill. *Modified from Zwick (2004).*

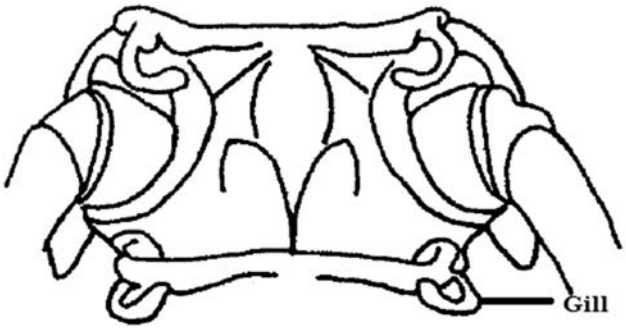


FIGURE 16.1.89 Perlodidae, *Megarcys ochracea* (Klapálek), thoracic gills (ventral). *Modified from Zhiltzova & Teslenko (1989).*

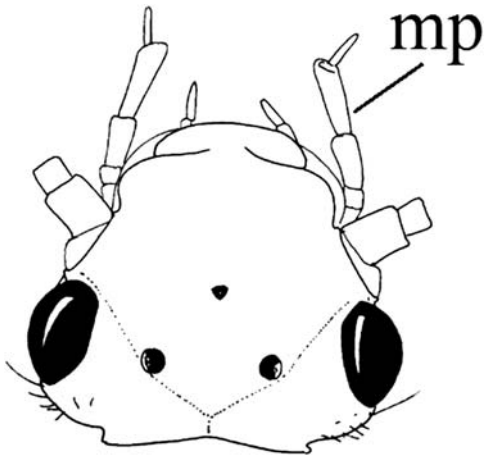


FIGURE 16.1.90 Chloroperlidae, head (dorsal). *Modified from Zwick (2004).*

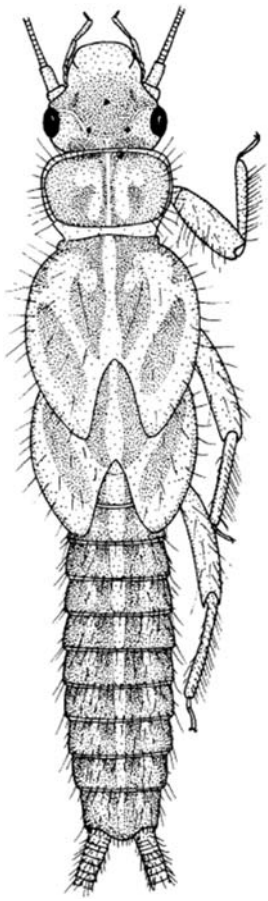


FIGURE 16.1.91 Chloroperlidae, habitus (dorsal). *Modified from Zwick (2004).*

Crustacea: Hexapoda: Insecta: Heteroptera: Families

This key is modified from Andersen (1996), DeWalt & Resh (2016), and Jansson (1996). Polhemus & Polhemus (2008) summarized the global diversity of aquatic true bugs. Keys to northern European aquatic bugs are available (Anderson 1996, Jansson 1996). Zheng et al. (1994) provided a key to adult aquatic Heteroptera for China. Some authors consider corixids of body length <5 mm with an exposed scutellum to constitute another family, Micronectidae, a small number of which occur in the Palaearctic.

1	Antennae shorter than head, inserted beneath eyes and (except Ochteridae) not visible from above (Figs. 16.1.92, 94 and 98)	2
1′	Antennae longer than head, inserted in front of eyes and visible from above (Figs. 16.1.100 and 103)	10
2(1)	Rostrum cylindrical or conical, distinctly of three or four segments (Fig. 16.1.94)	3
2′	Rostrum broad, blunt, and triangular, not distinctly segmented (Fig. 16.1.92); each front tarsus of one tarsomere, fringed with setae (Fig. 16.1.93)	Corixidae
3(2)	Apical abdominal respiratory appendages absent, or if present, short and flat (Fig. 16.1.96)	4
3′	Abdominal apex with a long, slender, tubular respiratory appendage (Fig. 16.1.95)	Nepidae
4(3)	Meso- and metathoracic legs fringed with swimming setae; ocelli absent; aquatic	5
4′	Meso- and metathoracic legs without swimming setae; ocelli usually present; riparian	9
5(4)	Dorsoventrally flattened, ovate insects (Figs. 16.1.97 and 104)	6
5′	Elongate or hemispherical insects, not flattened dorsoventrally (Figs. 16.1.98 and 99)	8
6(5)	Apical respiratory straps absent; eyes not protruding (Fig. 16.1.97); terminal instars and adults usually <16 mm	7

6′	Short, strap-like apical respiratory straps present (Fig. 16.1.96); eyes protrude from head margin; terminal instars and adults often >18 mm body length ..... Belostomatidae
7(6)	Habitus dorsoventrally flattened, elliptical (Fig. 16.1.97); rostrum reaching trochantin of mesothoracic legs; prothoracic legs raptorial; adults with wings; body length to 16 mm long ..... Naucoridae
7′	Habitus flattened, near circular (Fig. 16.1.104); rostrum reaching base of metathoracic coxae; legs not raptorial; adults apterous; up to 12 mm long ..... Aphelocheiridae
8(5)	Body hemispherical (Fig. 16.1.98); length <3 mm ..... Pleidae
8′	Body elongate (Fig. 16.1.99); length >5 mm ..... Notonectidae
9(4)	Profemora broad, raptorial; antennae concealed from above ..... Gelastocoridae
9′	Profemora slender, similar to other legs; antennae visible from above ..... Ochteridae
10(1)	Membrane of hemelytra without veins or with dissimilar sized cells; metacoxae small, conical; semiaquatic or riparian 11
10′	Membrane of hemelytra with four or five equal-sized cells (Fig. 16.1.100); metacoxae large, transverse; riparian ..... Saldidae
11(10)	Claws of at least protarsi inserted before apex (Fig. 16.1.101) 12
11′	Claws of all tarsi inserted at apex (Fig. 16.1.102) 13
12(11)	Metafemora long, greatly surpassing apex of abdomen ..... Gerridae
12′	Metafemora short, not, or only slightly surpassing apex of abdomen ..... Veliidae
13(11)	Head short and stout; eyes placed near posterior margin 14
13′	Head slender, as long as entire thorax; eyes set about halfway to base (Fig. 16.1.103) ..... Hydrometridae
14(13)	Body short, stout; ocelli present; antennae with 5 flagellomeres, distal three segments thinner than proximal two; head grooved ventrally to receive rostrum; two tarsomeres; <2.5 mm long ..... Hebridae
14′	Body elongate oval; ocelli absent; antennae with four antennomeres, basal segment longer than head; head not grooved ventrally; three tarsomeres; body length to 3.5 mm ..... Mesoveliidae

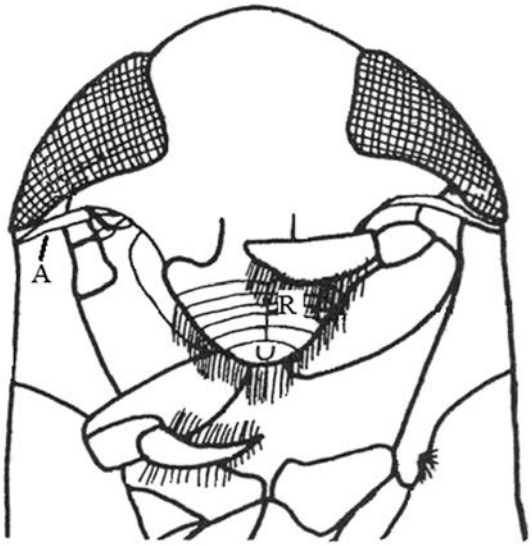


FIGURE 16.1.92 Corixidae; head and prothorax of *Sigara* (ventral view) showing rostrum (R) and antenna (A).

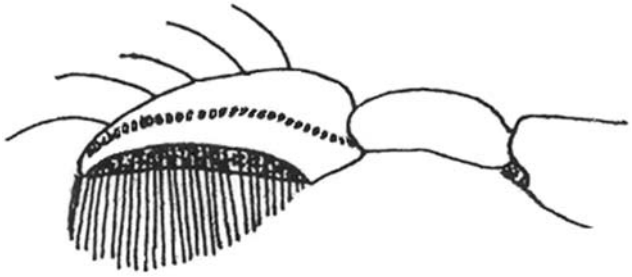


FIGURE 16.1.93 Corixidae; pala of male *Sigara*.

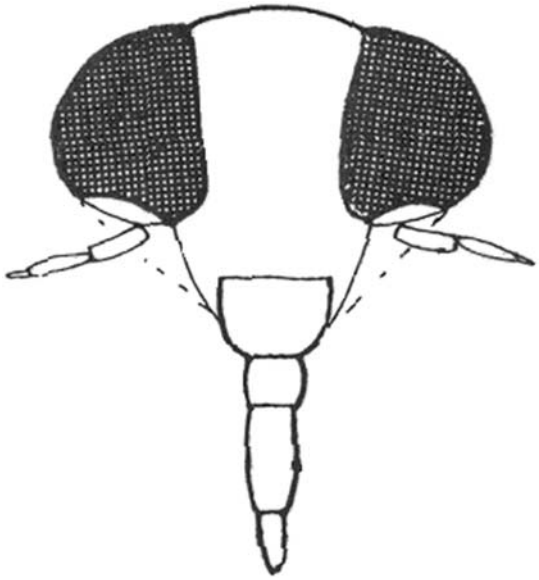


FIGURE 16.1.94 Notonectidae; head of *Notonecta* (ventral view) showing rostrum (R) and antenna (A).

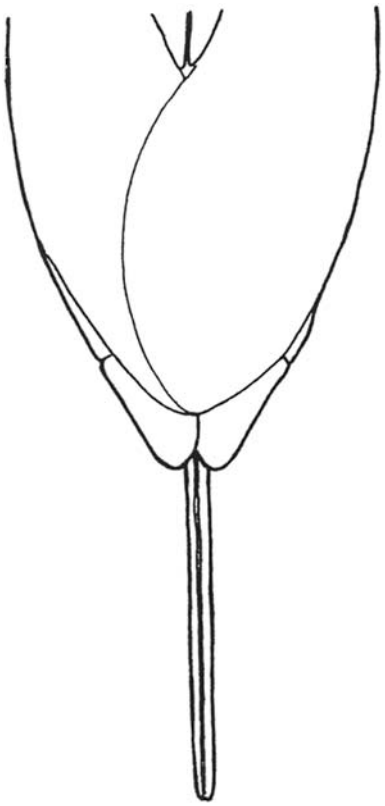


FIGURE 16.1.95 Nepidae; apex of abdomen of *Nepa* (dorsal view).

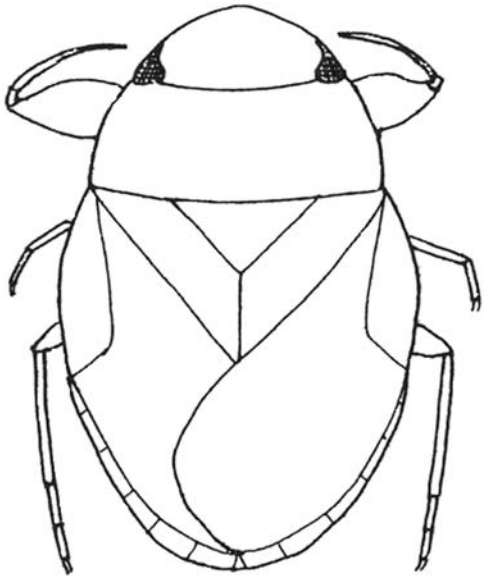


FIGURE 16.1.97 Naucoridae (dorsal view).

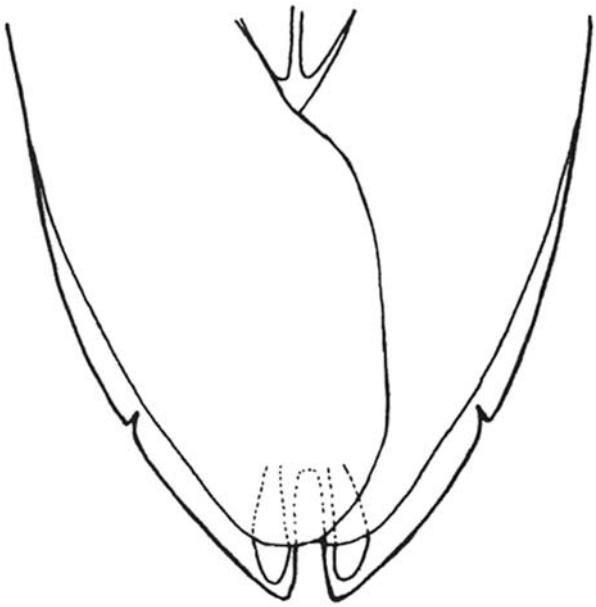


FIGURE 16.1.96 Belostomatidae; apex of abdomen of *Belostoma* (dorsal view).

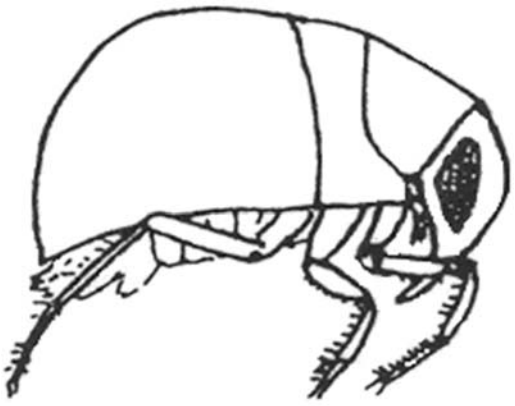


FIGURE 16.1.98 Pleidae (lateral view).

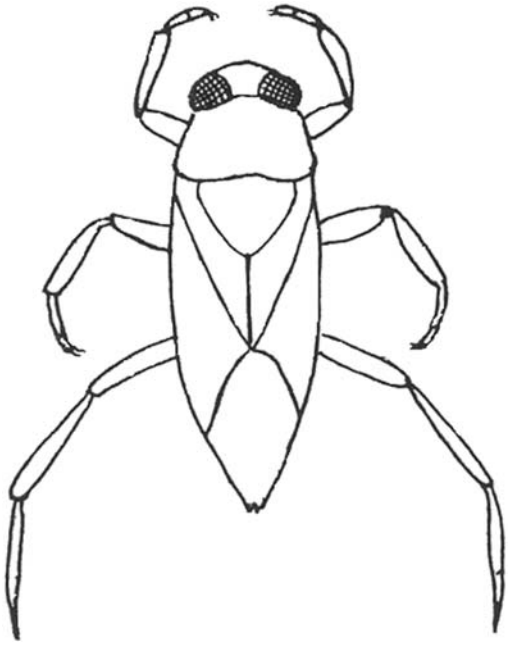


FIGURE 16.1.99 Notonectidae; *Notonecta* (dorsal view).

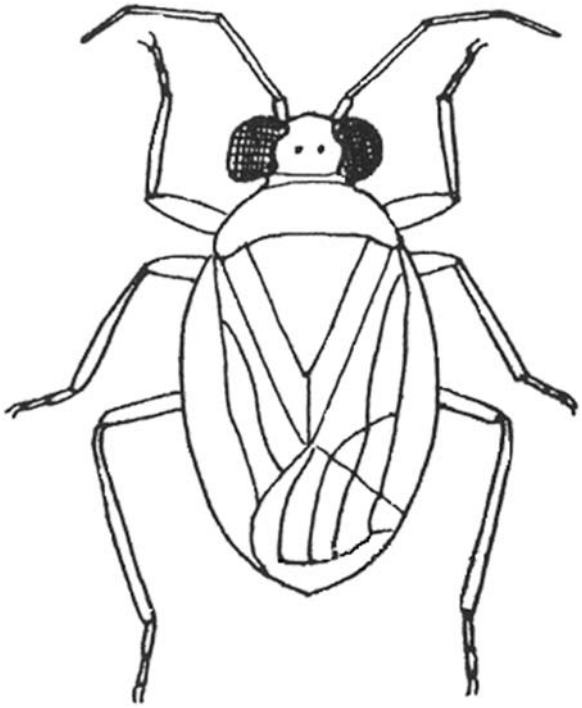


FIGURE 16.1.100 Saldidae; *Salda* (dorsal view) showing membrane (M).



FIGURE 16.1.101 Gerridae; protarsus.



FIGURE 16.1.102 Mesoveliidae; protarsus of *Mesovelia*.

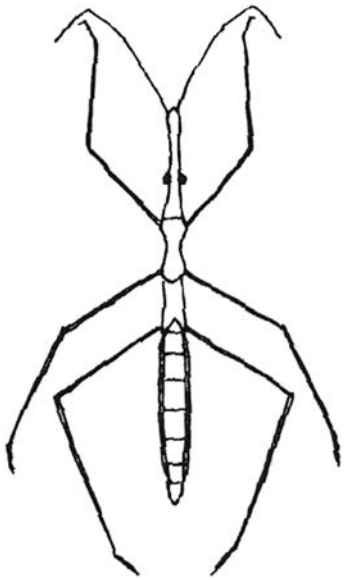


FIGURE 16.1.103 Hydrometridae; *Hydrometra* (dorsal view).

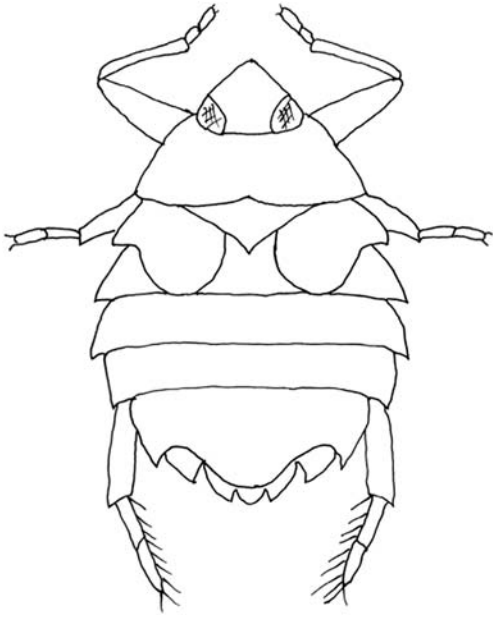


FIGURE 16.1.104 Aphelocheiridae; habitus *Aphelocheirus aestivalis* (dorsal view).

Hexapoda: Insecta: Megaloptera: Families

Megaloptera occur in both still and flowing waters. Cover & Resh (2008) discuss global diversity patterns of Megaloptera. Meinander (1996) provides a key to northern European families, genera, and species as larvae and adults. Yang & Yang (1994) present keys to Megaloptera adults and larvae, though several of the larvae of genera were not known at the time. Still, some are unknown. This key is modified from DeWalt & Resh (2016).

1 Abdominal segments 1−7 with lateral filaments lacking gill tufts at base, the last segment with a long, terminal filament that lacks prolegs or claws (Fig. 16.1.105); mature larvae to 1.5 cm ..... Sialidae, one genus: *Sialis*

1' Abdominal segments 1−8 with lateral filaments with or without gills tufts at base, last segment without a median filament, but with a pair of prolegs, each with a pair of claws (Fig. 16.1.106); larvae 3−8 cm long .....Corydalidae

Hexapoda: Insecta: Neuroptera: Families

This key is modified from Meinander (1996) and Yang and Yang (1994). Very few species of Neuroptera inhabit freshwaters, the most well-known being the Sisyridae, primarily for their peculiar habit of feeding and living in freshwater sponges. For this they have been given the common name of Spongillaflies. A few other families may be considered semiaquatic, living at the margins of waterbodies in decaying vegetation. Meinander (1996) provides a key to northern European families, genera, and species as larvae and adults. Yang & Yang (1994) present keys to adults and larvae at the genus level. Cover & Resh (2008) discuss global diversity patterns of Neuroptera.

1 Abdominal sterna lacking respiratory filaments; mandibles more robust, hooked medially near apex, and shorter than head (Fig. 16.1.108), or much longer than head and with at most a slight curve (Fig. 16.1.109); semiaquatic, found at edge of water in moist soil or leaves 2

1′ Abdominal sterna with seven pairs respiratory filaments; mouthparts a pair of long stylets much longer than head (Fig. 16.1.107); all tarsi with one claw; predatory on and inhabiting freshwater sponges ..... Sisyridae

2(1) Body slender; mandibles curved medially and near length of head (Fig. 16.1.108); prothorax narrower than the width of head ..... Neurorthidae

2′ Body wider; mandibles straight and longer than head (Fig. 16.1.109); prothorax as wide as head ..... Osmylidae

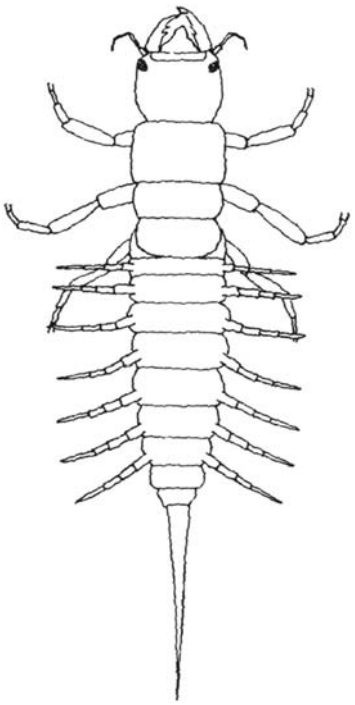


FIGURE 16.1.105 Sialidae, *Sialis* habitus (dorsal).

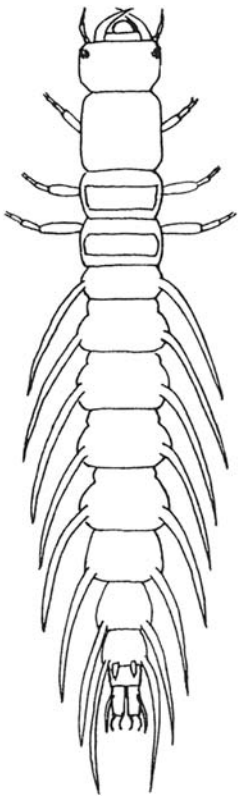


FIGURE 16.1.106 Corydalidae, generalize larva (dorsal).

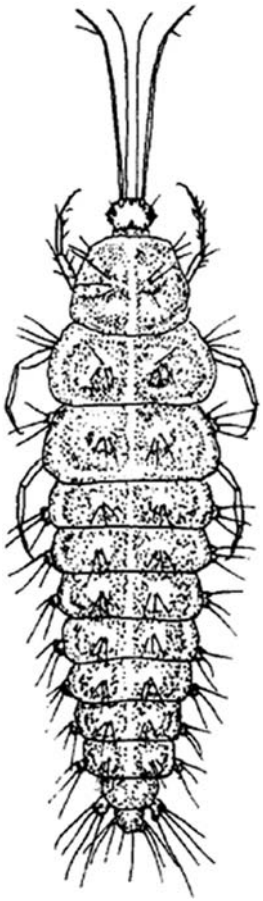


FIGURE 16.1.107 Sisyridae, *Sisyra* habitus (dorsal). *Modified from Meinander (1996).*

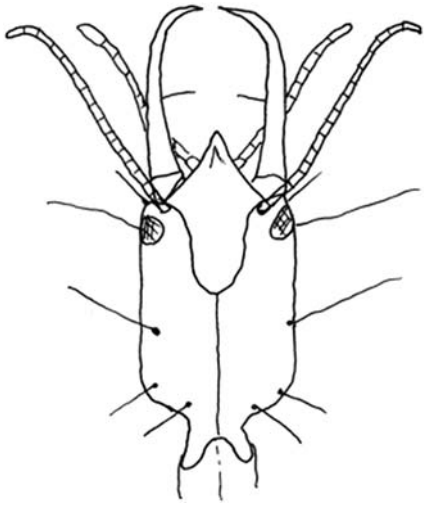


FIGURE 16.1.108 Neurorthidae; *Austroneurorthus* head and prothorax (dorsal). *Modified from Yang & Yang (1994).*

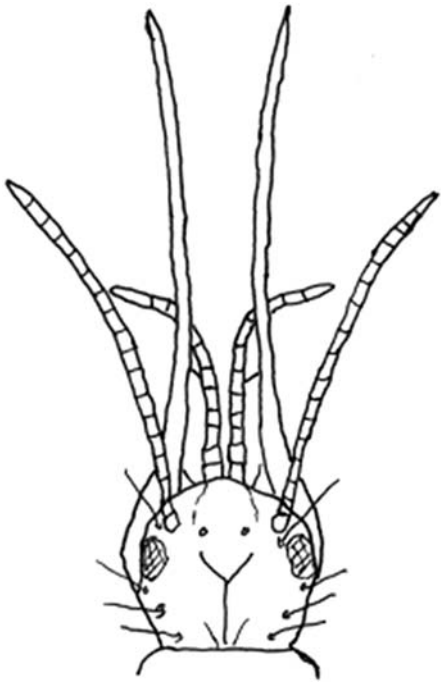


FIGURE 16.1.109 Osmylidae, *Osmylus* head (dorsal). *Modified from Yang & Yang (1994).*

Hexapoda: Insecta: Coleoptera: Families

This key is modified from DeWalt & Resh (2016), Nilsson (1996B), and White & Roughly (2008). Jäch & Balke (2008) present a global assessment of aquatic Coleoptera. They estimate that at least 3900 species are present in the Palaearctic, on par with the richest of biogeographical realms. Nilsson (1996B) provides an introduction to the aquatic beetles of northern Europe. He and several other authors provide treatments for larvae and adults of all families of aquatic Coleoptera for the region. Yang (1994) provides an impressive treatment of aquatic beetles in China. Adults in the following families are not keyed since they generally inhabit moist areas, but not within water: Limnichidae, Scirtidae, and Staphylinidae.

1	Elytra present, adults (Fig. 16.1.110) 2
1′	Elytra absent, larvae (Fig. 16.1.111) 21
2(1)	Elytra extensive, covering most segments; body size variable 3
2′	Elytra short, exposing two to four abdominal segments (Fig. 16.1.112); extremely small beetles, <1.5 mm long; all tarsi of three tarsomeres ..... Hydroscaphidae, one genus: *Hydroscapha*
3(2)	Compound eyes not divided into dorsal and ventral portions; meso- and metathoracic legs not shorter than prothoracic legs, not flattened 4
3′	Compound eyes divided into dorsal and ventral segments (Fig. 16.1.113); meso- and metathoracic legs shorter than prothoracic legs, extremely flattened, with tarsi flabelliform dorsal habitus dark ..... Gyrinidae
4(3)	Head not formed as a snout or beak; antennae not elbowed 5
4′	Head formed as a snout or beak anteriorly (Fig. 16.1.114); antennae geniculate after first long flagellomere ..... Curculionidae
5(4)	Antennae short and robust; distal segments dilated, clavate 6
5′	Antennae long and filiform 12
6(5)	Body glabrous with few hairs; flagellomere 2 not enlarged 7
6′	Dorsal body surface densely covered in erect setation (Fig. 16.1.115); flagellomere 2 enlarged to form a lamella (Fig. 16.1.116) ..... Dryopidae
7(6)	Antennae of six to nine flagellomeres; five abdominal sternites 8
7′	Antennal flagellomeres total nine, clavate and distal five flagellomeres pubescent (Fig. 16.1.117); six to seven abdominal sternites present ..... Hydraenidae
8(7)	Antennae of 7–9 flagellomeres, the distal three pubescent (Fig. 16.1.120); clypeus without broad emargination 9
8′	Antennae appearing as six flagellomeres, the distal five pubescent (Fig. 16.1.118); clypeus with broad emargination (Fig. 16.1.119) ..... Spercheidae
9(8)	Body elongate oval; head not concealed beneath pronotum, body outline being composed of three areas 10
9′	Body a wide oval; head concealed beneath pronotum, presenting only two general body regions (Fig. 16.1.121); granulate sculpture covers head and pronotum; elytra often with punctate rows ..... Georissidae, one genus: *Georissus*
10(9)	Pronotum not wider than long, without grooves 11
10′	Pronotum wider than long with conspicuous longitudinal grooves (Fig. 16.1.122) ..... Helophoridae, one genus: *Helophorus*
11(10)	Elongate body, with outline prominently interrupted between pronotum and elytra (Fig. 16.1.123); antennae inconspicuous, not longer than palps; pronotal width subequal to length, surface granular and with a medial, round depression; <5 mm ..... Hydrochidae
11′	Body oblong, little if any interruption of body outline (Fig. 16.1.124); antennae conspicuous and clubbed distally, as long or longer than palps; pronotum not much wider than long, smooth, no depression; up to 50 mm long ..... Hydrophilidae
12(5)	Antennal bases near head margin; hind tarsi clearly with five tarsomeres 3
12′	Antennal bases separated by no more than length of antennal flagellomere 1 (Fig. 16.1.125); metatarsus with four tarsomeres, or five if 4th is short and hidden in bilobed tarsomere 3; adults found on emergent vegetation ..... Chrysomelidae
13(12)	Metatarsi with tarsomere 5 as long as tarsomeres 1–4 combined, pronotum as broad as long 14
13′	Metatarsi with tarsomere 5 much shorter than combined tarsomeres 1–4 (Fig. 16.1.126) 15
14(13)	Body broadly oval, head covered by pronotum (Fig. 16.1.127); antennae subserrate to pectinate, much longer than head plus pronotum; adults found on emergent mineral and organic substrates at edge of water ..... Psephenidae
14′	Habitus narrower (Fig. 16.1.128); antennae filiform, not longer than head plus pronotum ..... Elmidae
15(13)	Metacoxal plates expanded to cover all or part of abdominal sternites 1 or 2 or 1–3 16
15′	Metacoxae not forming plates covering all or parts of abdominal sternites 1 or 2 or 1–3 17
16(15)	Hind coxal plates covering abdominal sternites 1 or 2, but exposing those segments laterally; bases of hind femora exposed; small (<1.5 mm length), black, oval, highly convex beetles; inhabit stream and lake margins ..... Sphaeriusidae, one genus: *Sphaerius*
16′	Hind coxal plates covering abdominal sternites 1–3 completely (Fig. 16.1.129); bases of hind femora hidden; larger beetles, elongate oval; elytra punctate, often spotted (Fig. 16.1.130) ..... Haliplidae

17(15) Eyes protuberant from head 18

17′ Eyes not protuberant from head 19

18(17) Body a rounded oval with posterior pronotal margin same width as anterior margin of elytra, elytra dark medially with margins in reddish-brown or yellowish (Fig. 16.1.131); often emits a rasping squeak when handled ..... Hygrobiidae, one genus: *Hygrobia* [China, Europe]

18′ Body elongate oval, posterior of pronotum much narrower than shoulders of elytra (Fig. 16.1.132) ..... Amphizoidae, one genus: *Amphizoa* [China]

19(17) Natatory setae present on all legs 20

19′ Natatory setae absent from legs (Fig. 16.1.133), crawling within rapidly flowing waters and hygropetric habitats ..... Aspidytidae, one species; *Aspidytes* wrasei Balke, Ribera, & Beutel, 2003 [China]

20(19) Metacoxal process wider than long with posterior margin V-shaped (Fig. 16.1.134); protibiae with large setae, curved spur, or hooked apex (Fig. 16.1.135); body convex dorsally, flattened ventrally; scutellum not visible; small, reddish beetles ≤5 mm long ..... Noteridae

20′ Metacoxal processes longer than wide (Fig. 16.1.136); convex on both dorsal and ventral surfaces; scutellum may be visible in larger specimens; body coloration varies greatly; body length also variable, sometimes exceeding 40 mm ..... Dytiscidae

21(1) Abdominal tergites 1−8 or 1 and 8 only with lateral digitiform articulated lobes; antennae reduced to two or three flagellomeres; larvae <3 mm, dorsoventrally compressed and found in wet films at margins of waterbodies 22

21′ Other combinations of digitiform lobes possible, or lacking; antennae with more than three flagellomeres; body shapes and habitats variable 23

22(21) Abdominal tergites 1−8 with lateral digitiform articulated lobes (Fig. 16.1.137); antennal segment length 2−3x> width, with a thin lateral appendage (Fig. 16.1.138) ..... Sphaeriusidae, one genus: *Sphaerius*

22′ Abdominal tergites 1 and 8 only with lateral digitiform articulated lobes (Fig. 16.1.139); antennae short, composed of two flagellomeres, one being short and broad, two much longer with distal sensory appendage adjacent to antenna (Fig. 16.1.140) ..... Hydroscaphidae, one genus: *Hydroscapha*

23(21) Thoracic legs always present, articulated with sternum; legs with six articles: coxa, trochanter, femur, tibia, tarsus, and one or two claws 24

23′ Thoracic legs present or not, if present leg composed of five articles: coxa, trochanter, femur, tibia, and single claw 30

24(23) Each leg with two claws; dorsum without tubercles or filaments 25

24′ Each leg with one claw; dorsum covered in small tubercles (Fig. 16.1.141) or long filaments (Fig. 16.1.142) ..... Haliplidae

25(24) Distal abdominal segment without hooks; abdominal segments lacking lateral filaments, or filaments on segments 1−6 only 26

25′ Abdomen with four conspicuous hooks on distal segment; nine abdominal segments, each with lateral filaments (Fig. 16.1.143) ..... Gyrinidae

26(25) Abdominal and thoracic terga not flattened and expanded laterally 27

26′ Abdominal and thoracic terga flattened and expanded laterally (Fig. 16.1.144) ..... Amphizoidae, one genus: *Amphizoa* [China]

27(26) Mandible long and curved with longitudinal groove (Fig. 16.1.147) 28

27′ Mandible short and stout with an expanded molar area (Fig. 16.1.145); urogomphi shorter than last abdominal segment; legs short, lacking swimming hairs, adapted for digging (Fig. 16.1.146) ..... Noteridae

28(27) Terminal abdominal segment usually shorter than urogomphi 29

28′ Terminal abdominal segment long, as long or longer than urogomphi, all three filaments densely packed with swimming hairs (Fig. 16.1.148) ..... Hygrobiidae, one genus: *Hygrobia* [China, Europe]

29(28) Frontoclypeolabrum without a short nasale flanked by lateral lobes; mandible lacking enlarged molar region (Fig. 16.1.147); urogomphi usually longer than last abdominal segment and often with seven long setae each, if shorter, legs are elongate with setal fringe for swimming ..... Dytiscidae

29′ Frontoclypeolabrum with a short nasale flanked by lateral lobes (Fig. 16.1.150); mandible with enlarged molar region with small teeth (Fig. 16.1.151); urogomphi longer than last abdominal segment with more than seven long setae each (Fig. 16.1.152); legs lack elongate setal fringe for swimming, crawls in fast water of cliff faces ..... Aspidytidae, one species; *Aspidytes wrasei* Balke, Ribera, & Beutel, 2003 [China]

30(23) Thoracic legs present and articulated at base 31

30′ Thoracic legs absent ..... Curculionidae

31(30)	Body elongate and sclerotized; no spines on last abdominal tergum 32
31′	All terga rounded and pale; larvae with two spines on last abdominal tergum (Fig. 16.1.153) ..... Chrysomelidae
32(31)	Antennae composed of three flagellomeres 33
32′	Antennae composed of 10 flagellomeres, filiform, as long as head and thorax combined (Fig. 16.1.154) ..... Scirtidae
33(32)	Abdominal sternum nine operculate, enclosing anal gills or not; terminal abdominal segment lacks urogomphi 34
33′	Abdominal sternum nine not operculate; most larvae have urogomphi 36
34(33)	Body cylindrical, triangular, or flattened (Figs. 16.1.111, 156 and 157) 35
34′	Body oval, flattened with broad lateral projections (Fig. 16.1.155); head concealed by pronotum; abdominal segment 9 broadly rounded ..... Psephenidae
35(34)	Body cylindrical, integument smooth (Fig. 16.1.157); segment 9 lacking retractile gills ..... Dryopidae
35′	Body triangular or flattened (Figs. 16.1.111 and 156), integument tuberculate; segment 9 with retractile gills ..... Elmidae
36(33)	Mandible without mola and prostheca (Fig. 16.1.161); labrum fused to clypeus (Fig. 16.1.162); maxilla with palpiger separated from stipes and appearing as another palpal segment (Fig. 16.1.163) 37
36′	Mandible with mola and prostheca (Fig. 16.1.158); labrum not fused to clypeus (Fig. 16.1.159); maxilla with palpiger not separated from stipes (Fig. 16.1.160) ..... Hydraenidae
37(36)	Abdominal segments 1−8 with well-developed spiracles (Fig. 16.1.164); segment 8 simple, not projecting above segment 9; abdominal segments lacking long, lateral filaments 38
37′	Abdominal segments 1−7 with reduced or vestigial spiracles; segment 8 with spiracles large, enclosed in spiracular atrium (Fig. 16.1.165), if cavity absent then spiracles reduced and abdominal appendages have long lateral filaments 39
38(37)	Urogomphi long, three segmented (Fig. 16.1.164); legs well developed ..... Helophoridae, one genus: *Helophorus*
38′	Urogomphi short, one segmented (Fig. 16.1.166); legs short, reduced segmentation ..... Georissidae, one genus: *Georissus*
39(37)	Maxilla stipes mesal face without lobe (Fig. 16.1.163); head with six stemmata 40
39′	Maxilla stipes mesal face with large lacinia-like lobe (Fig. 16.1.167); head with five well-separated stemmata on each side; lateral fleshy gills on abdominal segments 1−9; no urogomphi ..... Spercheidae
40(39)	Maxillary stipes with small setiferous tubercle on mesal face, palpiger without tubercle or appendage (Fig. 16.1.168); abdominal segments with complete tergal and sternal sclerites; mandibles inserted medially from antennal bases ..... Hydrochidae, one genus: *Hydrochus*
40′	Maxillary stipes lacking setiferous lobe (Fig. 16.1.163); abdominal segments with reduced tergal and sternal sclerites, normally divided into small sclerites, or sclerites absent entirely; segment 8 often with large, sclerotized tergal shield (Fig. 16.1.165) ..... Hydrophilidae

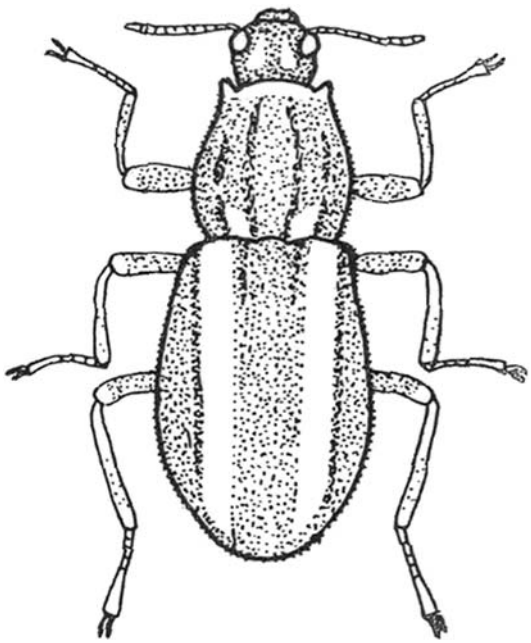


FIGURE 16.1.110 Elmidae, *Stenelmis* adult habitus (dorsal).

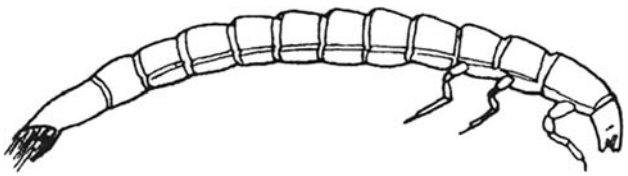


FIGURE 16.1.111 Elmidae, *Stenelmis* larval habitus (lateral).

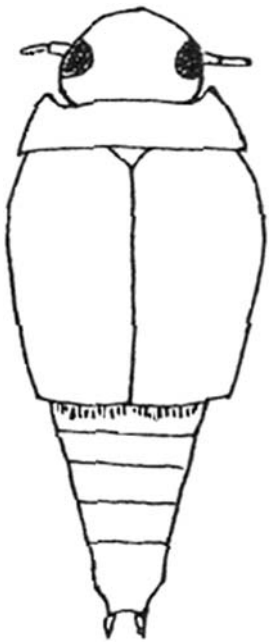


FIGURE 16.1.112 Hydroscaphidae, *Hydroscapha* adult habitus (dorsal).

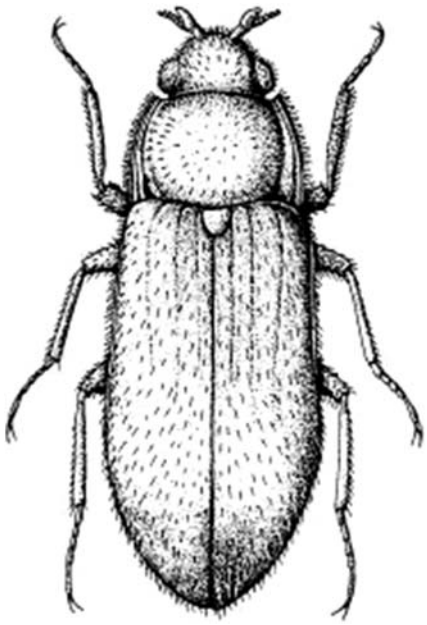


FIGURE 16.1.115 Dryopidae, *Dryops* adult habitus (dorsal). *Modified from Nilsson (1996B).*

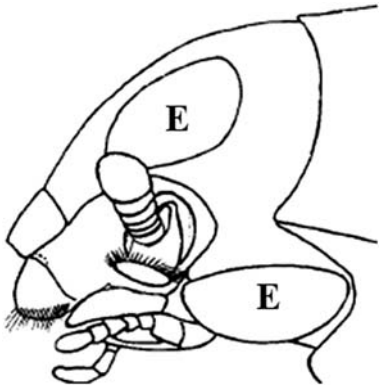


FIGURE 16.1.113 Gyrinidae, adult head, E compound eye (lateral). *Modified from Nilsson (1996B).*

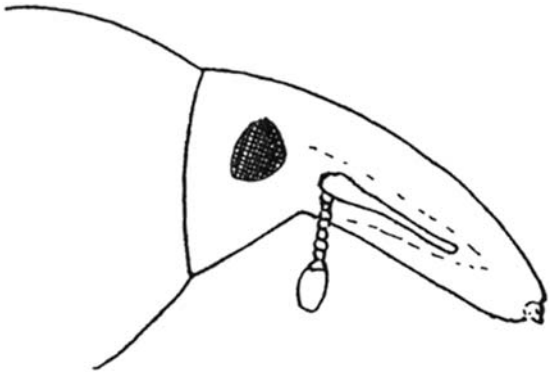


FIGURE 16.1.114 Curculionidae, adult head (lateral).

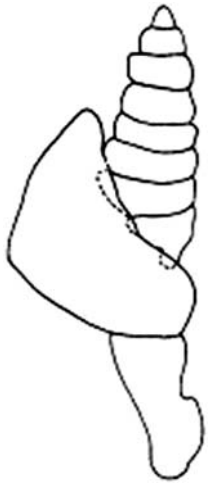


FIGURE 16.1.116 Dryopidae, *Dryops* adult antenna (dorsal). *Modified from Nilsson (1996B).*



FIGURE 16.1.117 Hydraenidae, adult, antenna (lateral). *Modified from Nilsson (1996B).*



FIGURE 16.1.118 Spercheidae, adult, antenna (lateral). *Modified from Nilsson (1996B).*

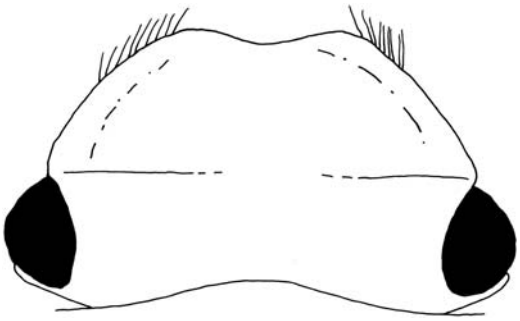


FIGURE 16.1.119 Spercheidae, adult, head with clypeal notch (dorsal). *Modified from Nilsson (1996B).*

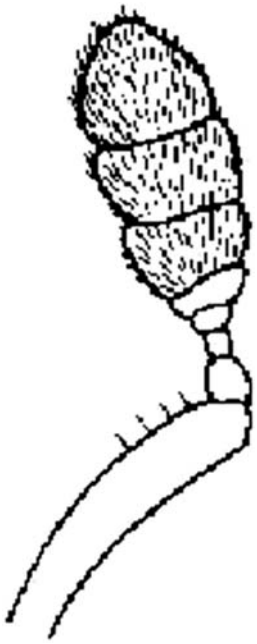


FIGURE 16.1.120 Hydrophiloidea, adult antenna (lateral). *Modified from Nilsson (1996B).*

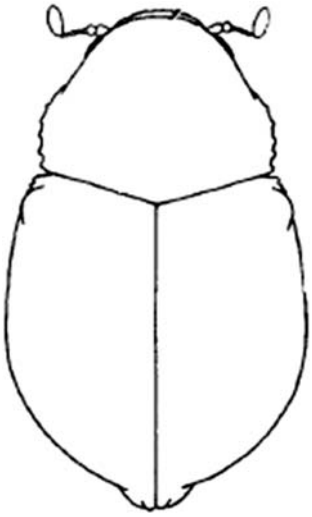


FIGURE 16.1.121 Georissidae, *Georissus* adult habitus (dorsal). *Modified from White & Roughley (2008).*

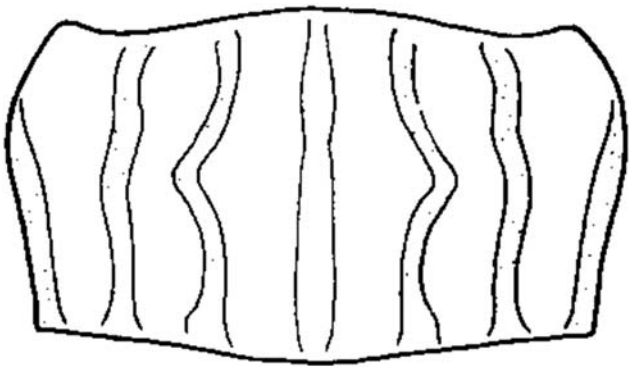


FIGURE 16.1.122 Helophoridae, *Helophorus* adult pronotum (dorsal).

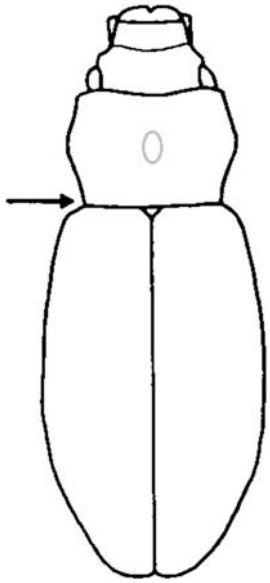


FIGURE 16.1.123 Hydrochidae, *Hydrochus* adult habitus (dorsal). Arrow indicates break in outline of body. *Modified from Nilsson (1996B) and Kriska (2014).*



FIGURE 16.1.125 Chrysomelidae, *Donacia*, anterior of head with antennal bases (dorsal). *Modified from Nilsson (1996B).*

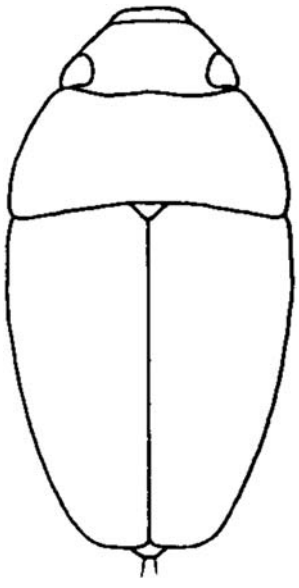


FIGURE 16.1.124 Hydrophilidae, adult habitus (dorsal).

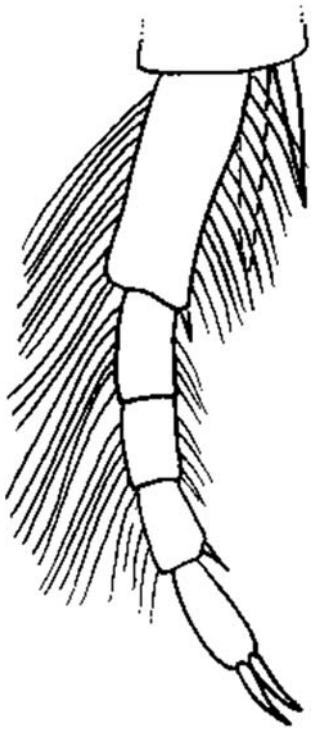


FIGURE 16.1.126 Dytiscidae, adult metatarsi (lateral).

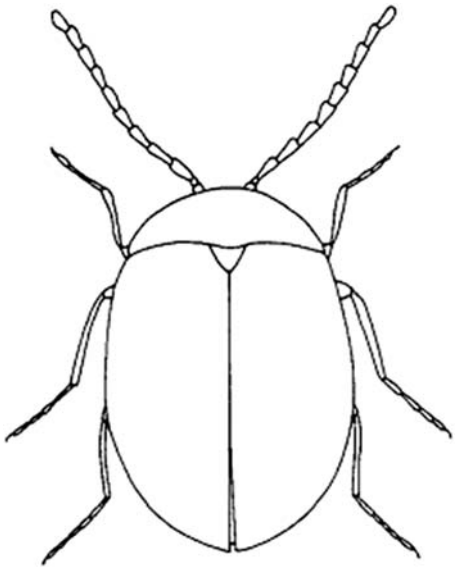


FIGURE 16.1.127 Psephenidae, adult habitus (dorsal).

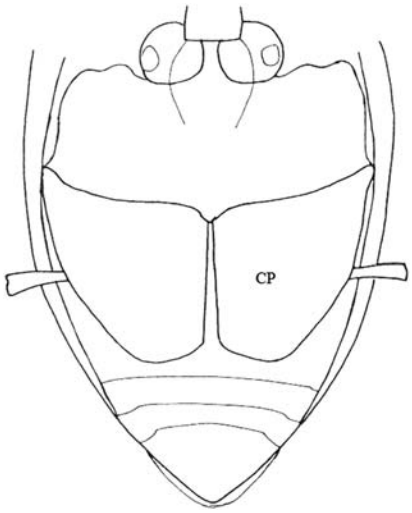


FIGURE 16.1.129 Haliplidae, *Haliplus* adult enlarged coxal plates (CP) (ventral).

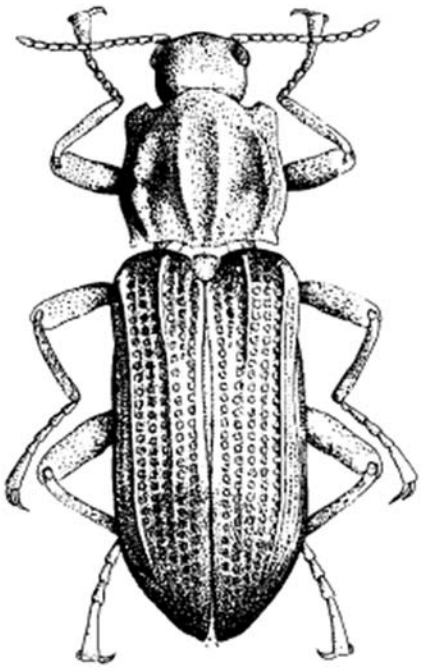


FIGURE 16.1.128 Elmidae, *Stenelmis* adult habitus (dorsal). *Modified from Nilsson (1996B).*

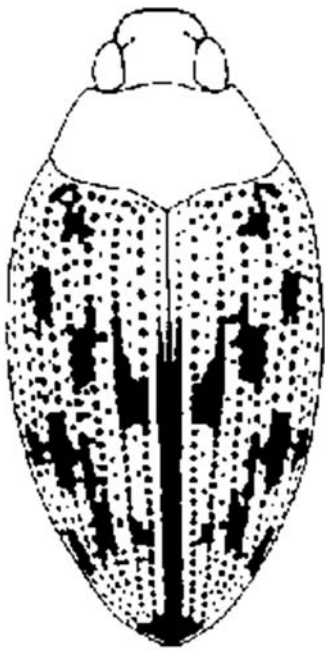


FIGURE 16.1.130 Haliplidae, adult habitus (dorsal). *Modified from Nilsson (1996B).*

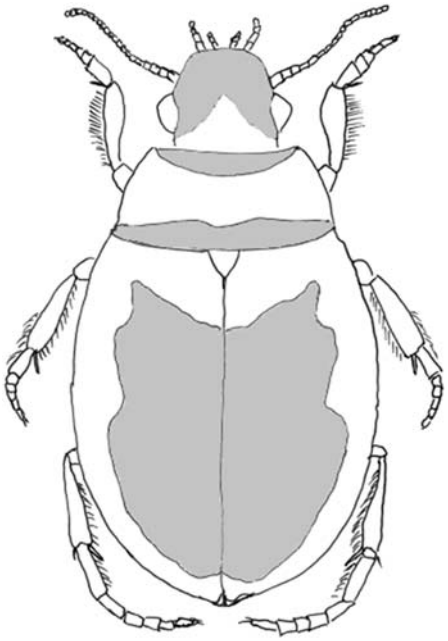


FIGURE 16.1.131 Hygrobiidae, *Hygrobia* adult (dorsal). *Modified from Kriska (2014).*

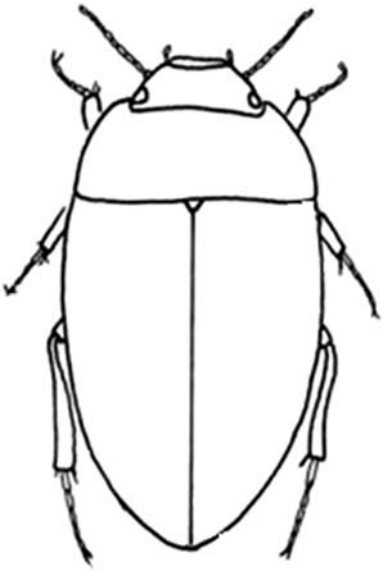


FIGURE 16.1.133 Aspidytidae, *Aspidytes* adult habitus (dorsal). Modified from Balke et al. (2005).

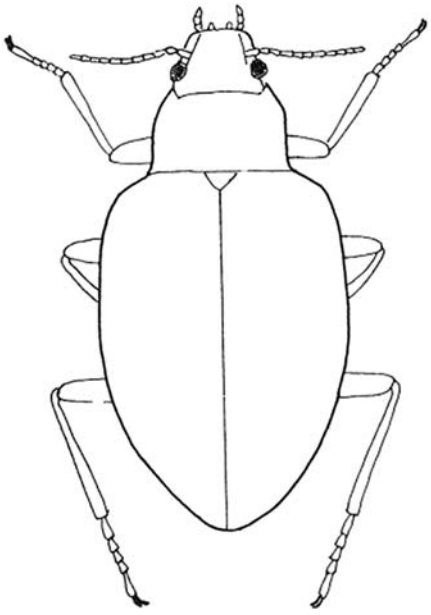


FIGURE 16.1.132 Amphizoidae, *Amphizoa* adult habitus (dorsal).

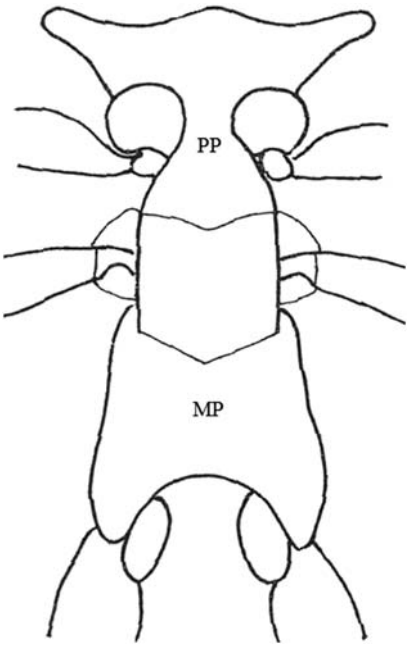


FIGURE 16.1.134 Noteridae, *Hydrocanthus* adult prosternal process (PP) and metasternal plate (MP) (ventral).

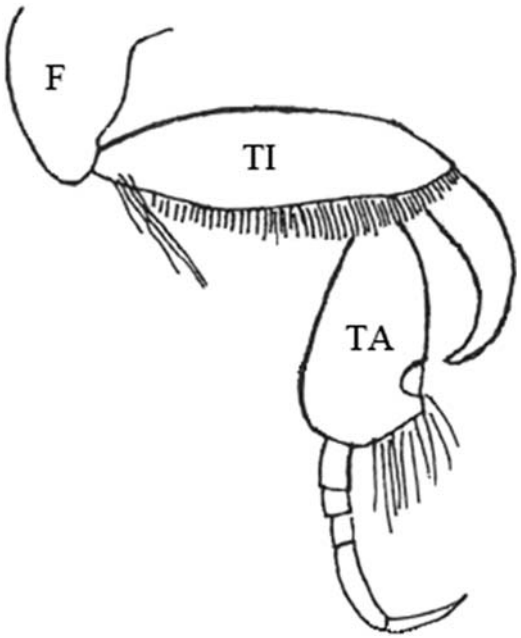


FIGURE 16.1.135 Noteridae, *Hydrocanthus* adult prothoracic leg (lateral). Profemur (F), tibia (TI), and tarsus (TA).

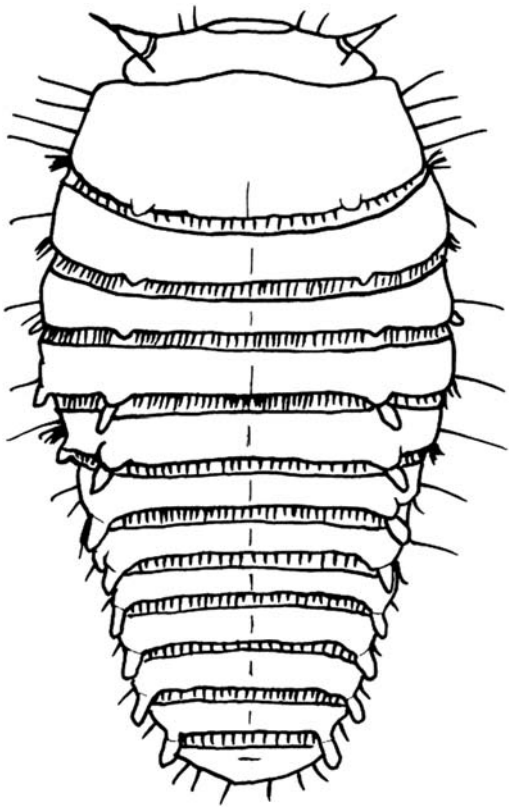


FIGURE 16.1.137 Sphaeriusidae, *Sphaerius* larva, half longitudinal (dorsal). Modified from Beutel & Leschen (2011).

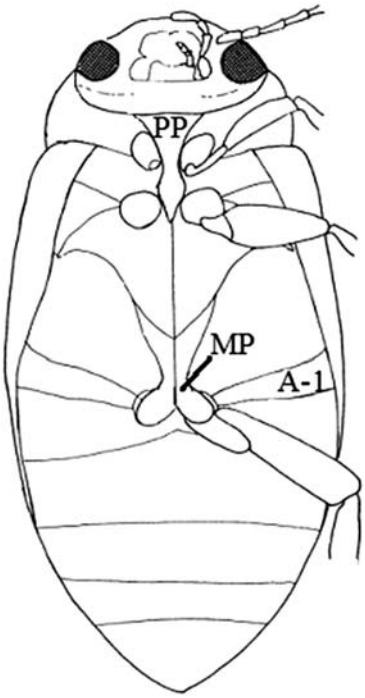


FIGURE 16.1.136 Dytiscidae, *Agabus* adult habitus (ventral). Prosternal process (PP), first abdominal sternum (A-1), and metacoxal process (MP).

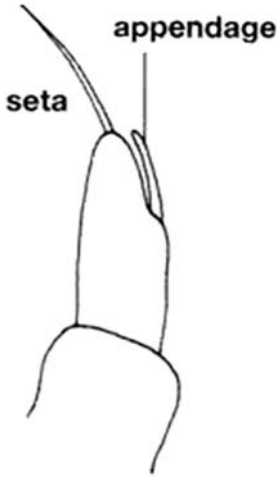


FIGURE 16.1.138 Sphaeriusidae, *Sphaerius* larval antenna (dorsal). *Modified from Beutel & Leschen (2011).*

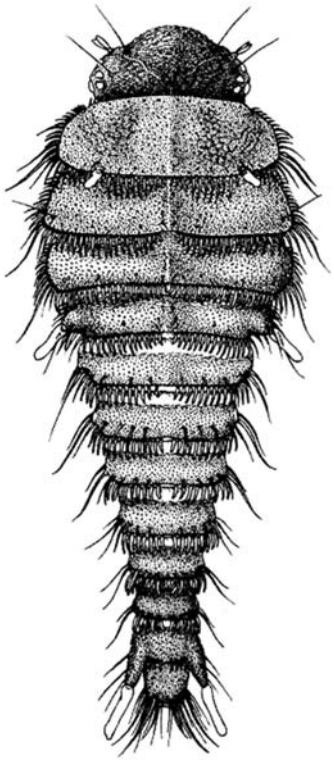


FIGURE 16.1.139 Hydroscaphidae, *Hydroscapha* larva habitus (dorsal). *Modified from White & Roughley (2008).*

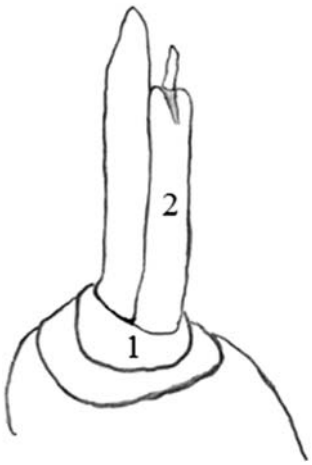


FIGURE 16.1.140 Hydroscaphidae, *Hydroscapha* larva, antenna (lateral). *Modified from Beutel & Haas (1998).*



FIGURE 16.1.141 Haliplidae, *Peltodytes* larval habitus (dorsal). *Modified from Nilsson (1996B).*

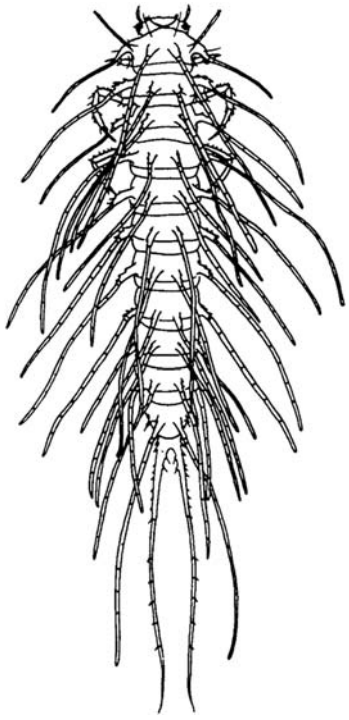


FIGURE 16.1.142 Haliplidae, *Haliplus* larval habitus (dorsal). *Modified from Nilsson (1996B).*

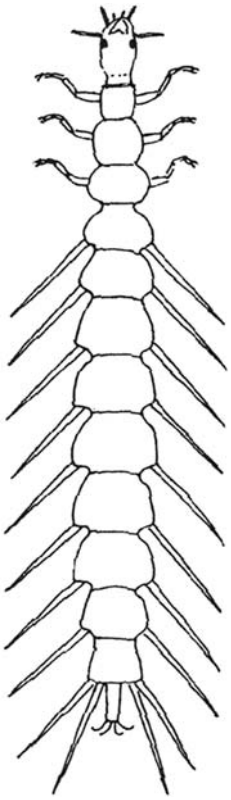


FIGURE 16.1.143 Gyrinidae, *Dineutus* larval habitus (dorsal).



FIGURE 16.1.145 Noteridae, larval mandible (dorsal). *Modified from Nilsson (1996B).*

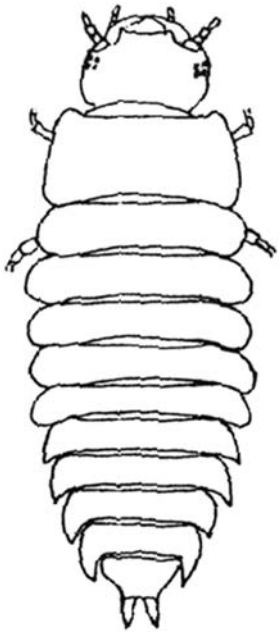


FIGURE 16.1.144 Amphizoidae, *Amphizoa* larval habitus (dorsal).

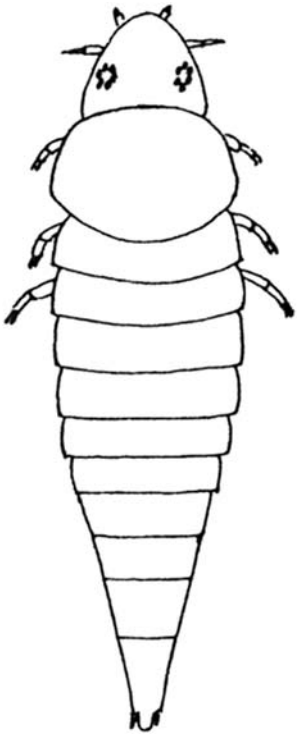


FIGURE 16.1.146 Noteridae, larval habitus (dorsal).



FIGURE 16.1.147 Dytiscidae, larval mandible (dorsal). *Modified from Nilsson (1996B).*

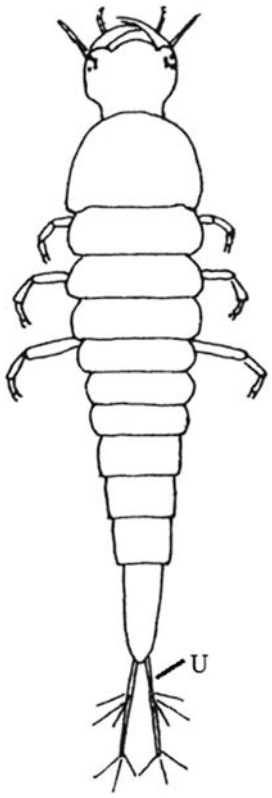


FIGURE 16.1.149 Dytiscidae, larval habitus (dorsal).

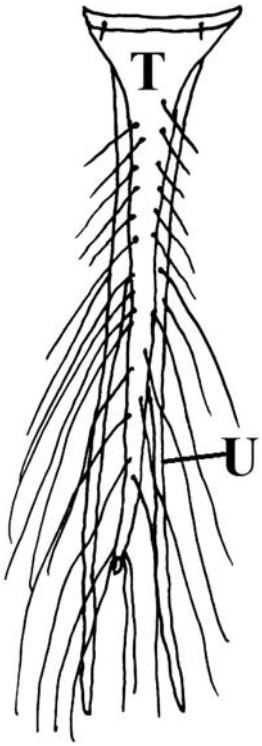


FIGURE 16.1.148 Hygrobiidae, *Hygrobia* larval terminal filament (dorsal). Terminal filament (T) and urogomphi (U).

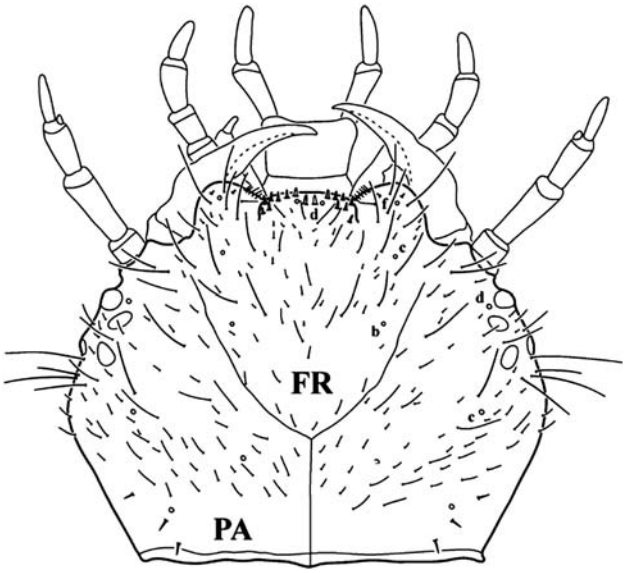


FIGURE 16.1.150 Aspidytidae, *Aspidytes* larval head (dorsal). *Modified from Michat et al. (2014). Frontoclypeolabrum (FR) and parietal (PA).*

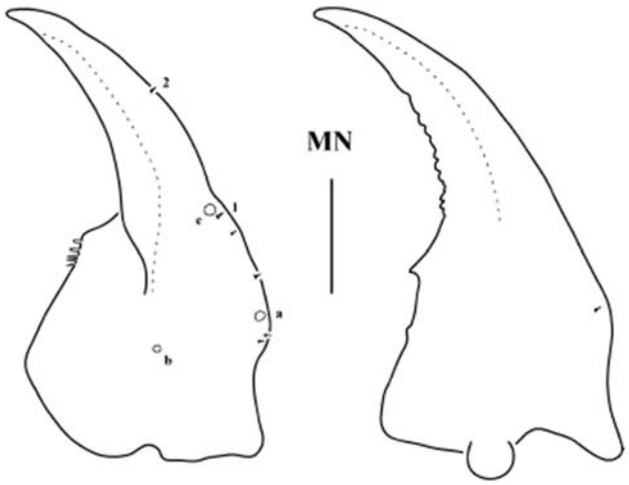


FIGURE 16.1.151 Aspidytidae, Aspidytes larval right and left mandibles (dorsal).

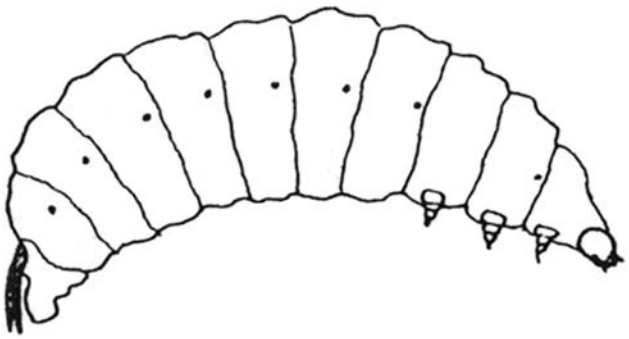


FIGURE 16.1.153 Chrysomelidae, *Donacia* larval habitus (lateral).

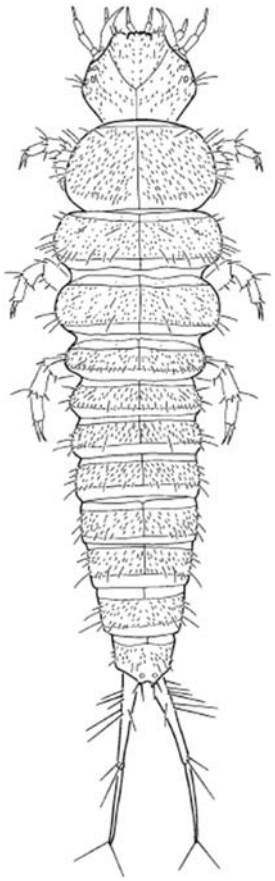


FIGURE 16.1.152 Aspidytidae, *Aspidytes* larval habitus (dorsal). *Modified from Michat et al. (2014).*

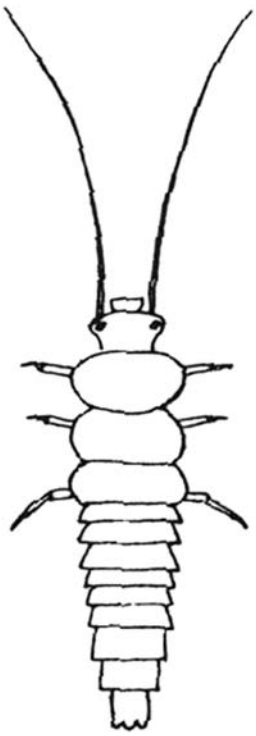


FIGURE 16.1.154 Scirtidae, *Cyphon* larval habitus (dorsal).

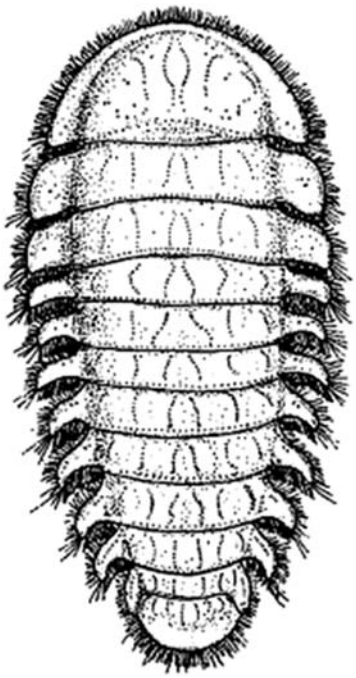


FIGURE 16.1.155 Psephenidae, *Eubria* habitus (dorsal). *Modified from Nilsson (1996B).*

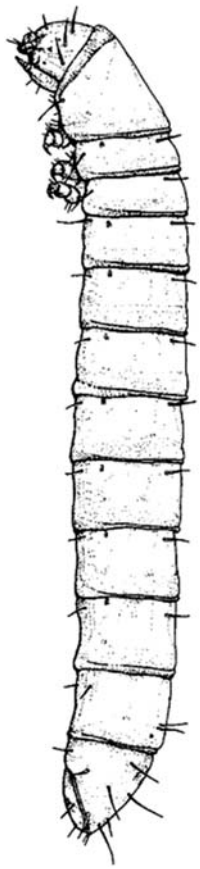


FIGURE 16.1.157 Dryopidae, *Dryops* larval habitus (lateral). *Modified from Nilsson (1996B).*



FIGURE 16.1.156 Elmidae, *Elmis* habitus (dorsal). *Modified from Nilsson (1996B).*



FIGURE 16.1.158 Hydraenidae, larval mandible with mola (M) and prostheca (P). *Modified from Nilsson (1996B).*

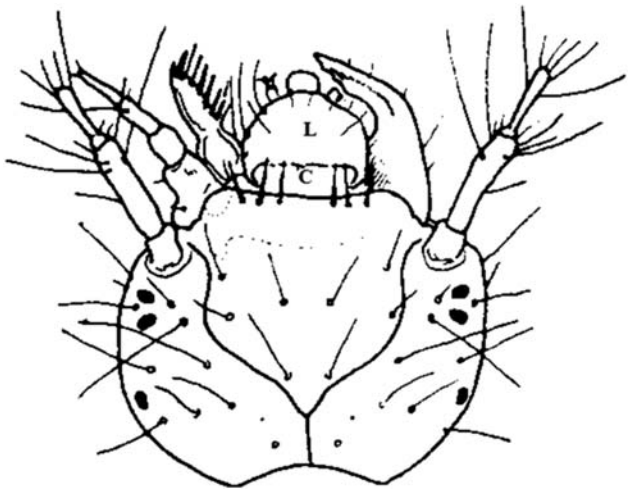


FIGURE 16.1.159 Hydraenidae, larval head (dorsal). *Modified from Nilsson (1996B).*



FIGURE 16.1.161 Hydrophilidae, larval mandibles.

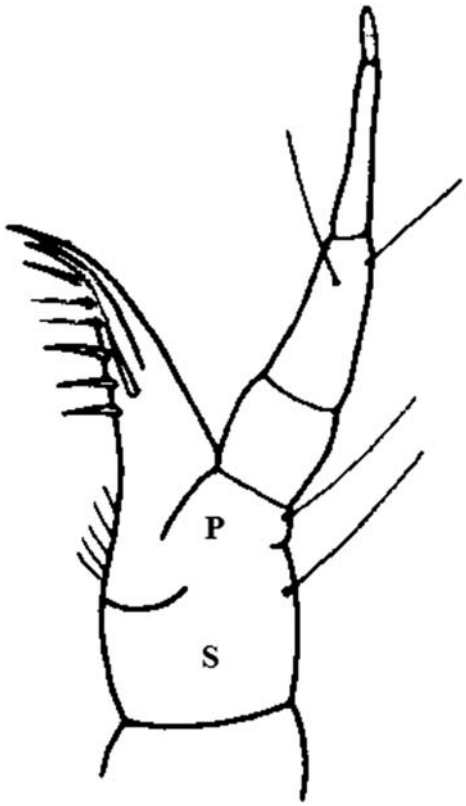


FIGURE 16.1.160 Hydraenidae, larval maxilla. *Modified from Nilsson (1996B).*

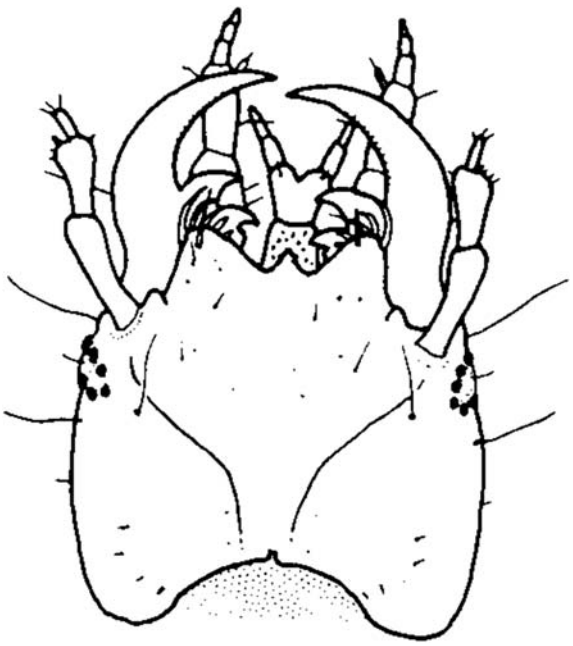


FIGURE 16.1.162 Helophoridae, *Helophorus* larval head (dorsal). *Modified from Nilsson (1996B).*

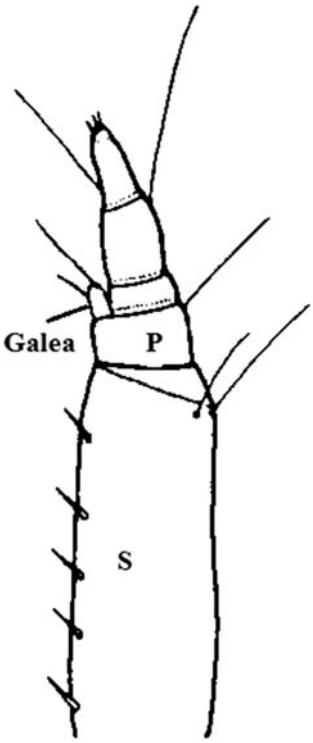


FIGURE 16.1.163 Hydrophilidae, larval maxilla (dorsal). *Modified from Nilsson (1996B).*

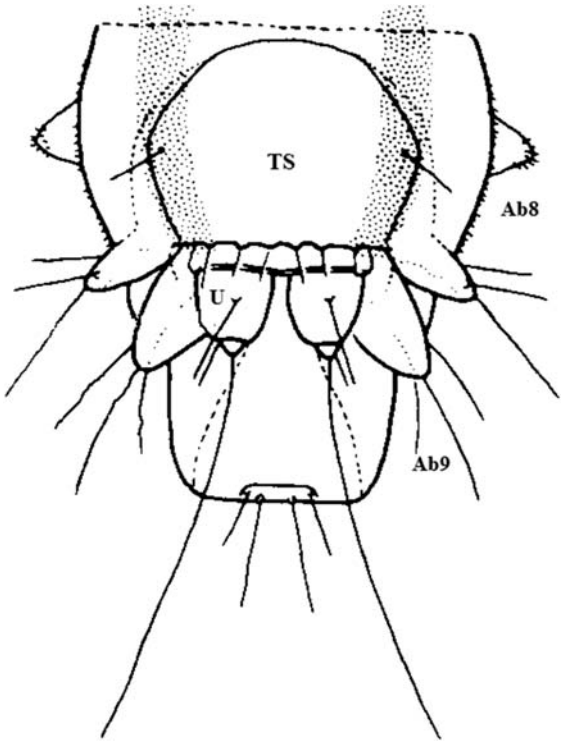


FIGURE 16.1.165 Hydrophilidae, *Enochrus* larval terminalia (dorsal). Tergal shield (TS), urogomphi (U), and eighth abdominal segment (Ab8). *Modified from Nilsson (1996B).*

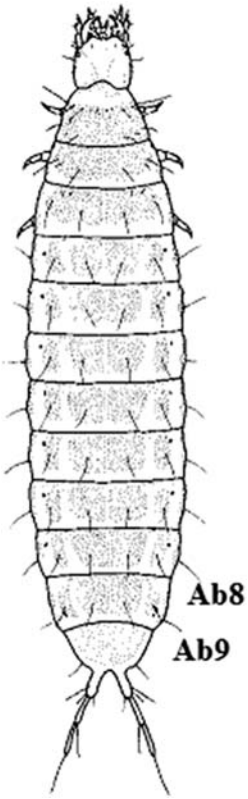


FIGURE 16.1.164 Helophoridae, *Helophorus* habitus (dorsal). Eighth (Ab8) and ninth (Ab9) abdominal segments.

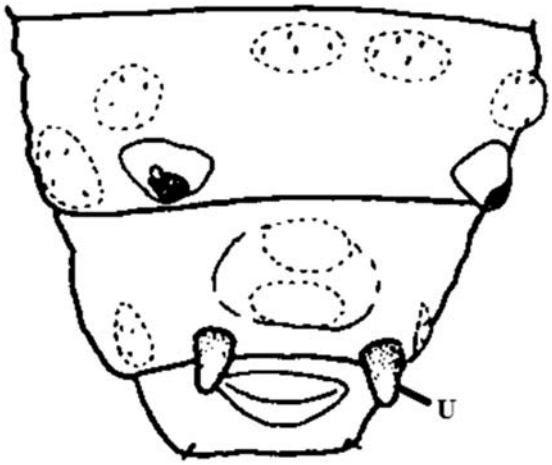


FIGURE 16.1.166 Georissidae, *Georissus* larval terminalia (dorsal). Urogomphi (U).

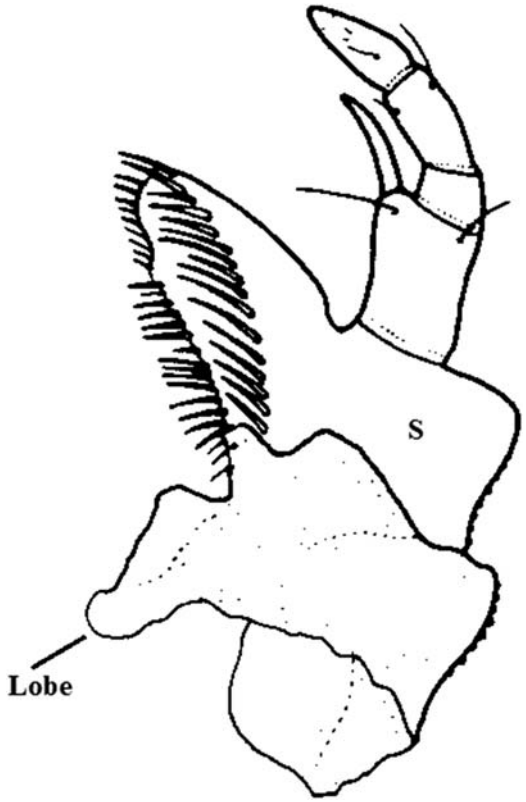


FIGURE 16.1.167 Spercheidae, larval maxilla (dorsal) showing location of median lobe of stipes (S). Modified from Nilsson (1996B).

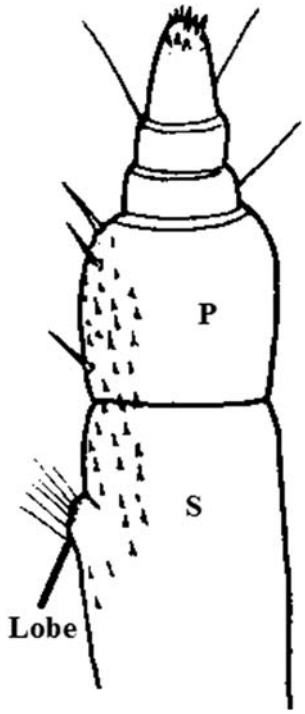


FIGURE 16.1.168 Hydrochidae, *Hydrochus* larval maxilla (dorsal). Lateral lobe of stipes (S) and palpiger (P). Modified from Nilsson (1996B).

Crustacea: Hexapoda: Insecta: Trichoptera: Families

We have accepted the classification presented in Holzenthal et al. (2007), including: Ptilocoleptidae as a subfamily of Hydroptilidae, Arctopsychidae as a subfamily within the Hydropsychidae, and Thremmatidae as a subfamily within Uenoidae, some of which conflicts with that presented in World Trichoptera Checklist (http://entweb.sites.clemson.edu/database/trichopt). Important literature that should be consulted include de Moor & Ivanov (2008) who presented a synopsis of the global diversity and distribution of Trichoptera; Waringer & Graf (2013) who published a synoptic key to families and genera of Europe; Wiggins et al. (1994) who provided a dichotomous key to families and genera occurring in China; and Solem & Gullefors (1996) who presented a key to larvae of northern Europe. Distributions of families, where they are limited to a portion of the Palaearctic, are from Holzenthal et al. (2007). A highly valued resource is that of Wiggins (2004) where larval representatives of all caddisfly families are diagnosed, illustrated, and keyed. An extensive discussion of the entire order is presented in Holzenthal et al. (2015). This key is modified from DeWalt & Resh (2016), Morse et al. (1994), Solem & Gullefors (1996), Waringer & Graf (2013), and Wiggins & Currie (2008).

1	Anal claws hamulate, with or without inner teeth (Fig. 16.1.171); case not spiral, or absent 2
1′	Anal claws hamulate, medial surface with large, irregular teeth (Fig. 16.1.169); larval case spiral, made of sand grains (Fig. 16.1.170) ..... Helicopsychidae, one genus: *Helicopsyche*
2(1)	All thoracic nota covered by sclerites (Fig. 16.1.172) 3
2′	Metanotum entirely or mostly membranous, possibly having only scattered setae or small plates (Figs. 16.1.173 and 174) 5
3(2)	Abdomen lacking branched gills and setal tufts on anal prolegs 4
3′	Abdomen and last two thoracic segments with ventral branched gills (Fig. 16.1.175); mature larvae >5−20 mm long; anal prolegs long, claws long, their bases attended by setal tufts; larvae form attached silk and debris retreats and erect mesh capture nets; common in running waters and in some wave-swept shores of large lakes ..... Hydropsychidae
4(3)	Ab9 tergum with wide sclerite (Fig. 16.1.176); mature larvae <5 mm long; anal prolegs short and with a stout claw; fifth instar larvae with swollen abdomen and living in a case—prior instars free living; case cylindrical or sacculate (Figs. 16.1.177 and 178) ... Hydroptilidae
4′	Abdominal tergum 9 entirely membranous; mature larvae >5 mm long; anal prolegs elongate with a projecting claw (Fig. 16.1.179); abdomen not enlarged; larvae construct sand tubes on hard substrates (as in Fig. 16.1.197) ..... Ecnomidae, one genus: *Ecnomus* [Widespread]
5(2)	Antennae shorter, ≤3x long as wide, or absent (Fig. 16.1.182); mesonotum without curved or angled bars; with or without case 6



FIGURE 16.1.169 Helicopsychidae, *Helicopsyche* larval case.



FIGURE 16.1.170 Helicopsychidae, *Helicopsyche* anal claw (lateral).

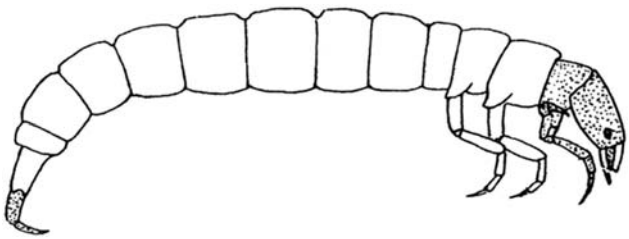


FIGURE 16.1.171 Polycentropodidae, larval habitus (lateral).

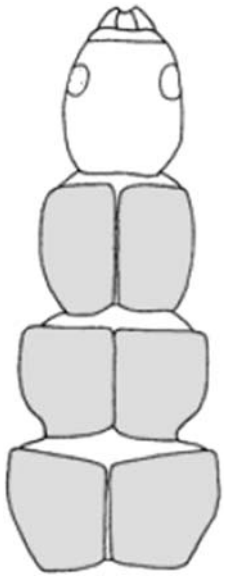


FIGURE 16.1.172 Hydroptilidae head and thorax (dorsal). *Modified from Bouchard (2009).*

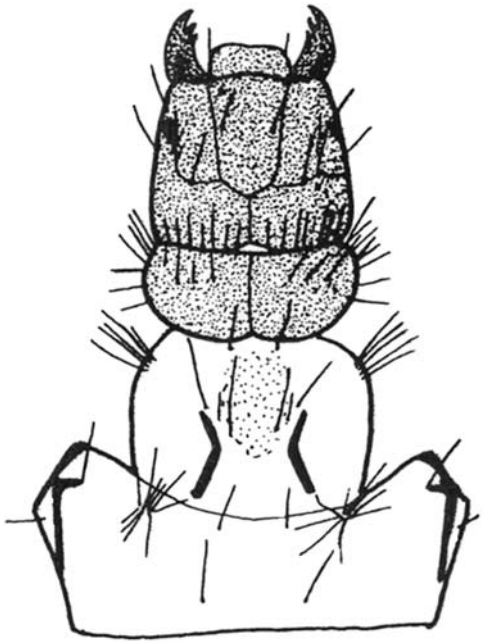


FIGURE 16.1.173 Leptoceridae, *Ceraclea* head and thorax (dorsal).

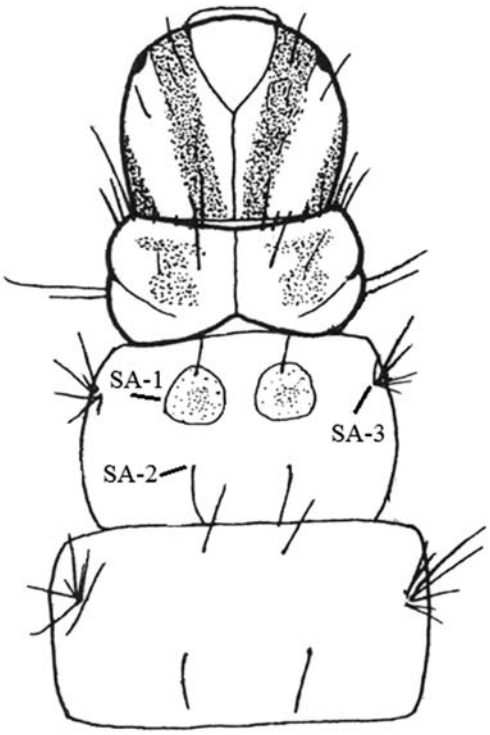


FIGURE 16.1.174 Phryganeidae, *Ptilostomis*, larval head and thorax (dorsal).



FIGURE 16.1.175 Hydropsychidae, larval habitus (lateral). *Modified from Bouchard (2009).*

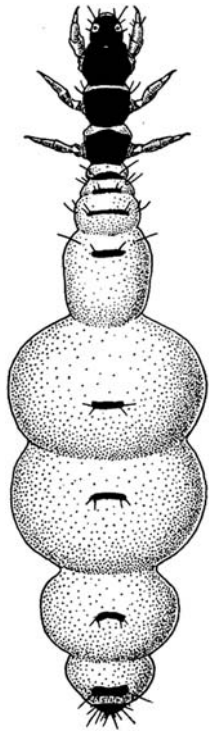


FIGURE 16.1.176 Hydroptilidae, *Leucotrichia* habitus (dorsal).

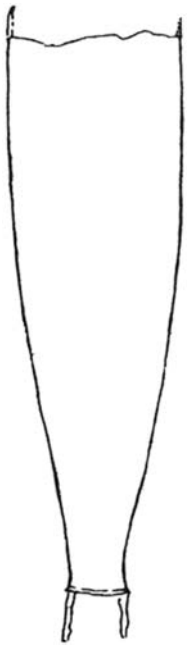


FIGURE 16.1.177 Hydroptilidae, *Oxyethira* barrel-shaped silk case (lateral).



FIGURE 16.1.178 Hydroptilidae, *Hydroptila* purse-like case (lateral).

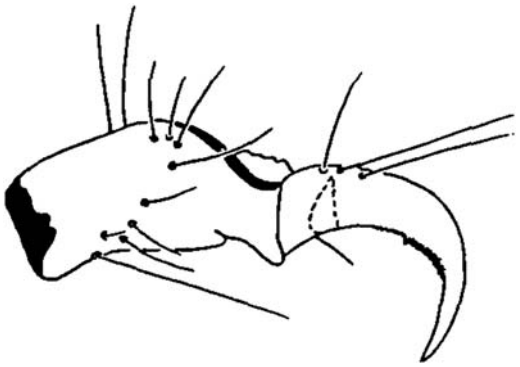


FIGURE 16.1.179 Ecnomidae, anal proleg (lateral). *Modified from Barnard & Clark (1986).*



FIGURE 16.1.180 Leptoceridae, *Oecetis* head and antenna (A) (lateral).

5′	Antennae relatively long, ≥6x long as wide (Fig. 16.1.180); and/or mesonotum membranous with a pair of curved or angled bars (Fig. 16.1.173); larvae build cases of various materials and shapes (Fig. 16.1.181) ..... Leptoceridae
6(5)	Mesonotum largely or entirely membranous (Fig. 16.1.183), or with only small sclerites covering not more than half of notum (Fig. 16.1.184); pronotum never with an anterolateral projection; larvae with or without a case 7
6′	Mesonotum with conspicuous sclerotized plates (Fig. 16.1.185); pronotum sometimes with transverse pronotal groove and anterolateral projection (Fig. 16.1.186) 17
7(6)	Abdominal tergum 9 bearing a sclerotized dorsal plate; with or without portable case 8
7′	Abdominal tergum 9 entirely membranous; no portable case 11
8(7)	Prosternal horn absent; metanotal SA-3 without a sclerite and usually with a single seta; case, if present, of sand and pebbles, domed cases or free living 9
8′	Prosternal horn present (Fig. 16.1.187); metanotal SA-3 usually consisting of a small sclerite and a cluster of setae (Figs. 16.1.183 and 184); case a cylinder, usually of vegetation, spiral and concentric ring designs ..... Phryganeidae
9(8)	Anal proleg free for most its length, claws as long as elongate sclerite on anal legs; larvae without a case, but larvae construct fixed domed cases as pupal cases 10
9′	Anal proleg mostly fused to segment 9, claws much shorter than the elongate sclerite on anal legs (Fig. 16.1.188); larvae with turtle-like case of coarse sand with ventral strap of sand (Fig. 16.1.189) ..... Glossosomatidae
10(9)	Tibiae, tarsi, and claws of prothoracic legs articulating with femora to form chelate legs (Fig. 16.1.190) ..... Hydrobiosidae, one genus: *Apsilochorema* [China, southeast Russia]
10′	Profemora not chelate, normal for order ..... Rhyacophilidae
11(7)	Labrum sclerotized and rounded, conspicuous (Fig. 16.1.192) 12
11′	Labrum membranous and T-shaped (Fig. 16.1.191), sometimes withdrawn in preserved specimens; head without markings; protrochantin poorly developed; larvae construct fixed, silken retreats on undersides of rocks and wood ..... Philopotamidae
12(11)	Abdomen with lateral fringe (Fig. 16.1.193) 13
12′	Abdomen without lateral fringe 15
13(12)	Body medium-sized; head length and width nearly equal 14
13′	Body length to 40 mm, head prolonged, more than 2 times as long as wide (Fig. 16.1.194) .... Stenopsychidae, one genus: *Stenopsyche* [East Asia]
14(13)	Mesopleuron extended anteriorly as a lobate process, tibiae and tarsi of all legs fused (Fig. 16.1.195); metathoracic trochantin subacute; larvae construct fixed tube of sand in small streams ..... Xiphocentronidae, one genus: *Melanotrichia* [China]
14′	Mesopleuron not extended anteriorly; tibiae and tarsi separate on all legs; prothoracic trochantin broad and securiform, separated from episternum by a dark suture (Fig. 16.1.196); larvae construct tubular retreats on rocks and logs (Fig. 16.1.197) ..... Psychomyiidae
15(12)	Pronotum not extended ventroposteriorly as lobate process; trochantin of prothoracic leg with acute apex, fused completely with episternum and lacking separating suture (Fig. 16.1.198); larvae construct a variety of silken retreats (Fig. 16.1.199), or tubes buried in sand (Fig. 16.1.200) 16
15′	Pronotum extended ventroposteriorly, partially covering fore coxae (Fig. 16.1.195); larvae construct sand tubes on hard substrates (as in Fig. 16.1.197) ..... Ecnomidae

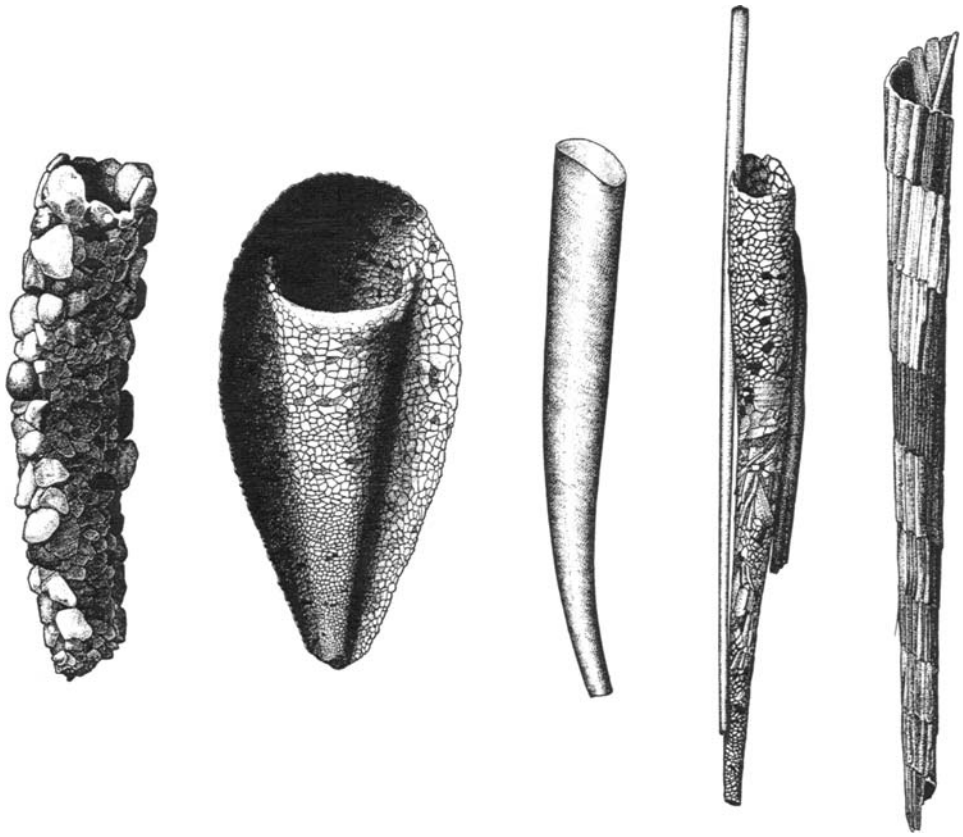


FIGURE 16.1.181 Leptoceridae, variety of cases. *Modified from Wiggins (2004).*

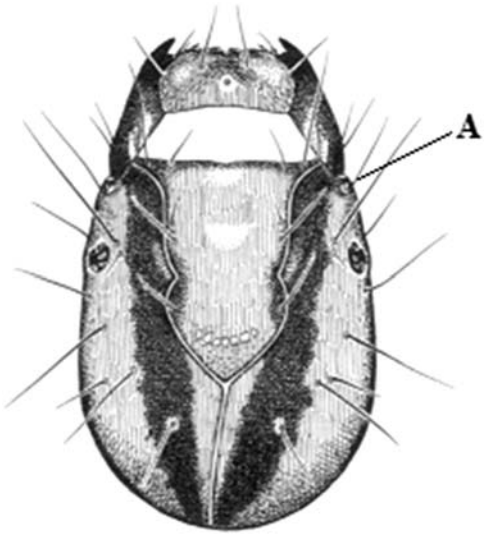


FIGURE 16.1.182 Phryganaeidae, *Agrypnia* head and antenna (A) (dorsal). *Modified from Wiggins (2004).*

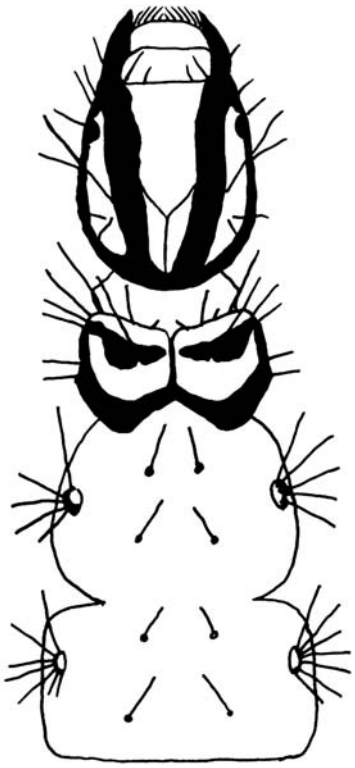


FIGURE 16.1.183 Phryganaeidae, head and thorax (dorsal). *Modified from Wiggins (1994).*

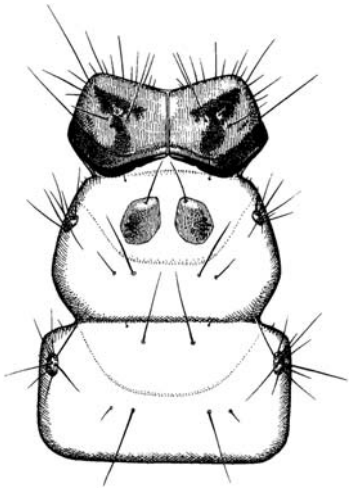


FIGURE 16.1.184 Phryganaeidae, *Oligostomis* head and thorax (dorsal). *Modified from Wiggins et al. (1994).*

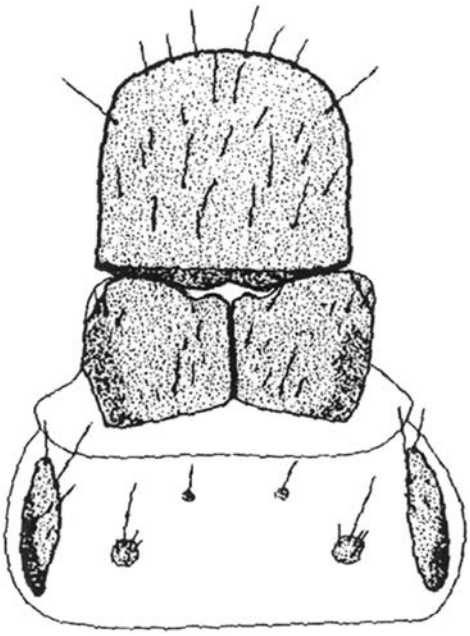


FIGURE 16.1.185 Uenoidae, *Neophylax* thoracic nota (dorsal).

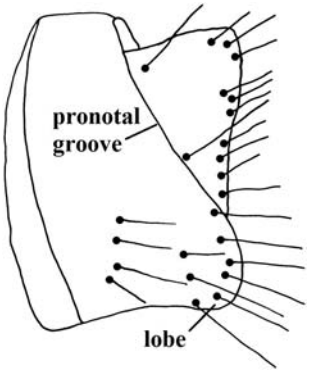


FIGURE 16.1.186 Lepidostomatidae, *Lepidostoma*, pronotum (lateral). *Modified from Wiggins et al. (1994).*



FIGURE 16.1.187 Phryganaeidae, prosternal horn (ventral). *Modified from Wiggins et al. (1994).*

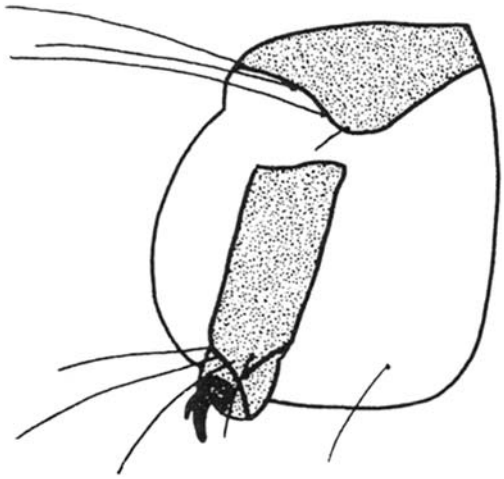


FIGURE 16.1.188 Glossosomatidae, anal proleg (lateral).

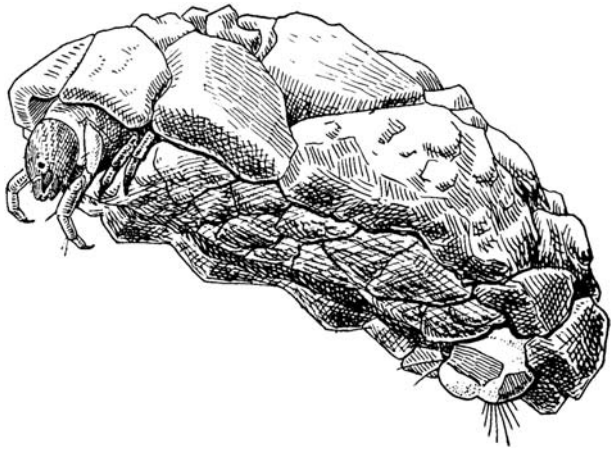


FIGURE 16.1.189 Glossosomatidae, tortoise case (ventrolateral). *Modified from Ross (1944).*

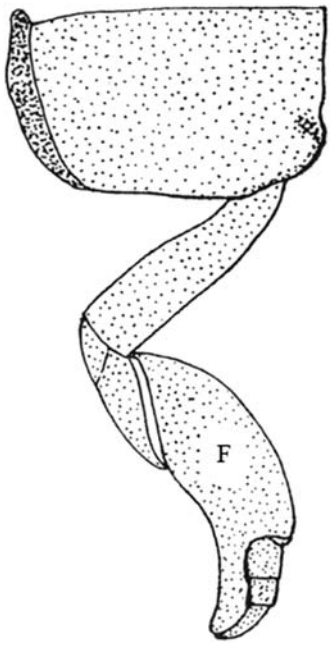


FIGURE 16.1.190 Hydrobiosidae, prothoracic leg (lateral).

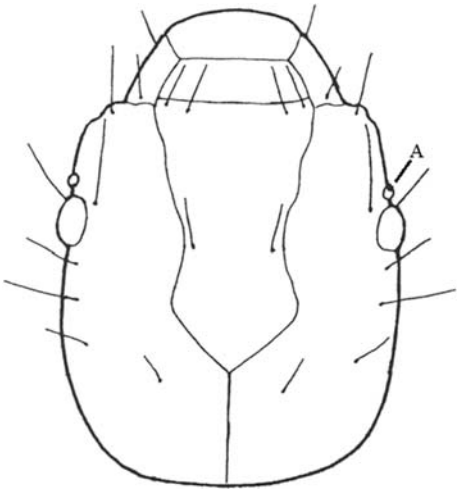


FIGURE 16.1.192 Lepidostomatidae, *Lepidostoma*, head (dorsal).

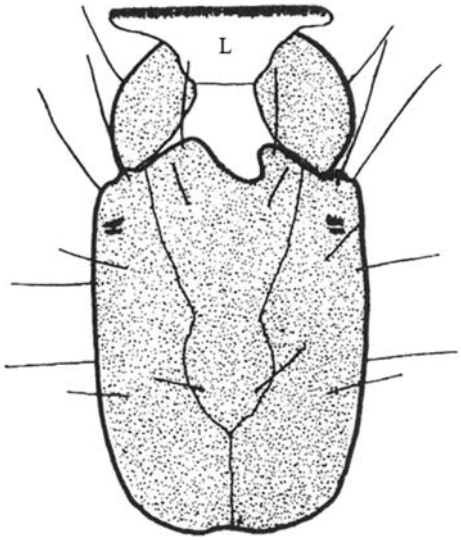


FIGURE 16.1.191 Philopotamidae, *Chimarra* with T-shaped labrum (dorsal).

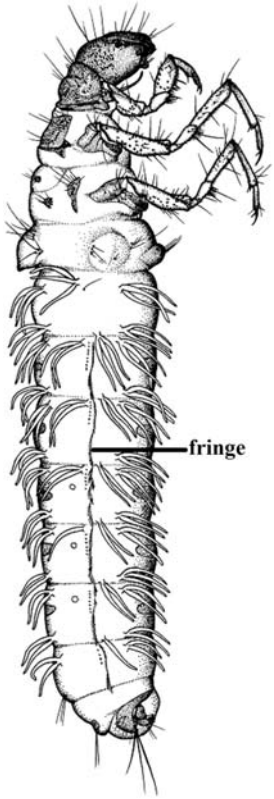


FIGURE 16.1.193 Limnephilidae, *Anabolia*, Ab1–5 with lateral fringe of hairs (lateral). *Modified from Wiggins (2004).*

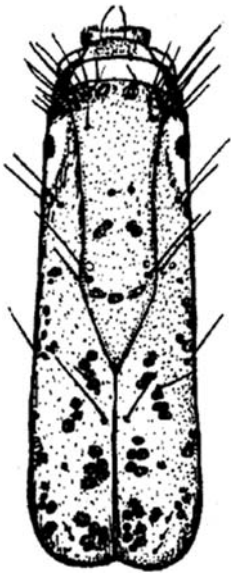


FIGURE 16.1.194 Stenopsychidae, *Stenopsyche* head (dorsal). *Modified from Wiggins et al. (1994).*

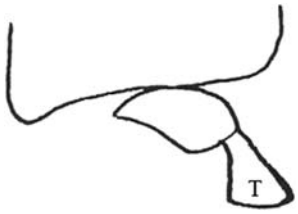


FIGURE 16.1.196 Psychomyiidae, pronotum and trochantin (T) (lateral).

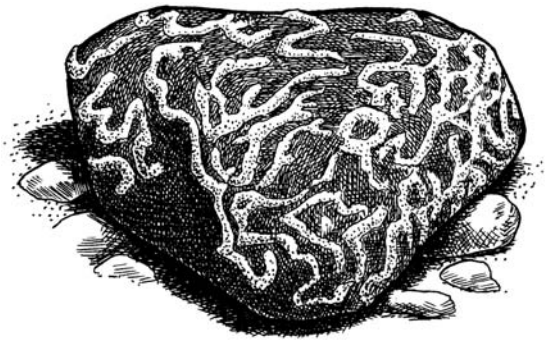


FIGURE 16.1.197 Psychomyiidae, silk and mineral retreats on rock. *Modified from Wiggins (2004).*

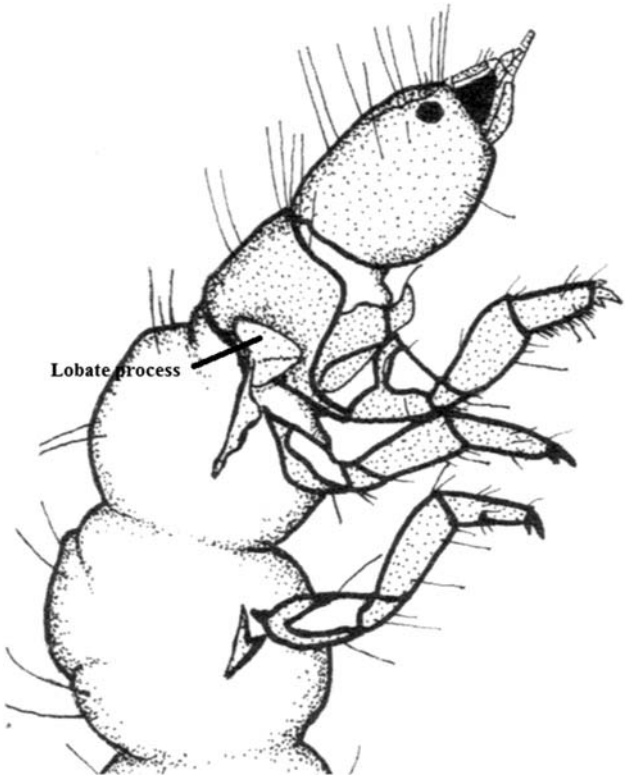


FIGURE 16.1.195 Xiphocentronidae, *Melanotrichia serica* Barnard & Dudgeon head and thorax (lateral). *Modified from Dudgeon (1999).*

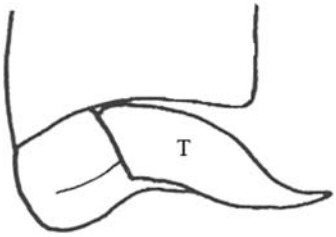


FIGURE 16.1.198 Polycentropodidae, *Polycentropus* prothoracic trochantin (T).

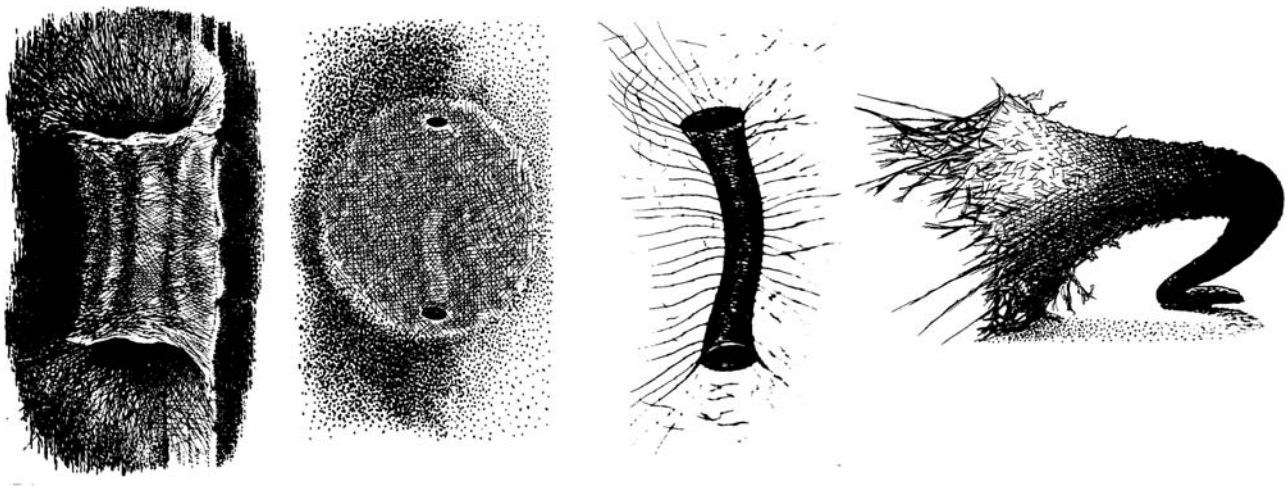


FIGURE 16.1.199 Polycentropodidae, silk retreat types. *Modified from Wiggins (2004).*

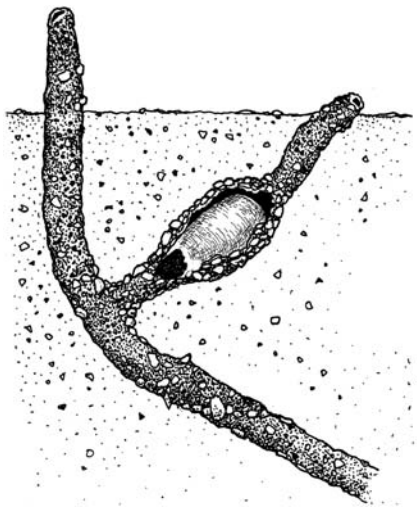


FIGURE 16.1.200 Dipseudopsidae, sand retreat. *Modified from Wiggins et al. (1994).*

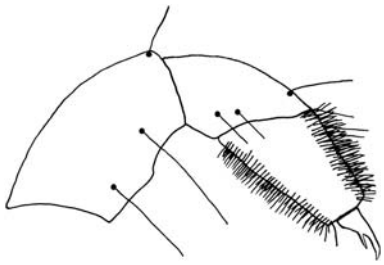


FIGURE 16.1.201 Dipseudopsidae, *Phylocentropus* prothoracic tibiae and tarsi (dorsal).

16(15)	Tarsi broader than their tibiae and flattened (Fig. 16.1.201); retreats of branching tubes in sand (Fig. 16.1.200) ..... Dipseudopsidae
16′	Tarsi narrower than tibiae and cylindrical; retreats of unbranched silken tubes on surfaces of rocks and wood (Fig. 16.1.199) ..... Polycentropodidae
17(6)	Ab1 always with lateral humps, but may lack dorsal hump; metanotal SA-1 always present, usually with small sclerite and from one to several setae 18
17′	Ab1 lacking dorsal and lateral humps (Fig. 16.1.202); metanotal SA-1 entirely lacking (Fig. 16.1.203) or composed of a single seta without sclerite; pronotum with transverse sulcus; cases may be cylindrical-tapering or four-sided ..... Brachycentridae
18(6)	Claws of metathoracic legs as long as those on mesothoracic legs; case never of sand with lateral flanges 19
18′	Claws of metathoracic legs a short stub or a slender filament (Fig. 16.1.204), different from that of other legs; case of sand with lateral flanges and a hood ..... Molannidae
19(18)	Anterolateral angles of pronotum if produced, not divergent; labrum without a dorsal row of long setae; case of various materials 20
19′	Anterolateral angles of pronotum produced and divergent; row of approximately 16 stout setae across middle of labrum (Fig. 16.1.205); flattened case of leaves or bark (often flanged), or a hollowed twig ..... Calamoceratidae

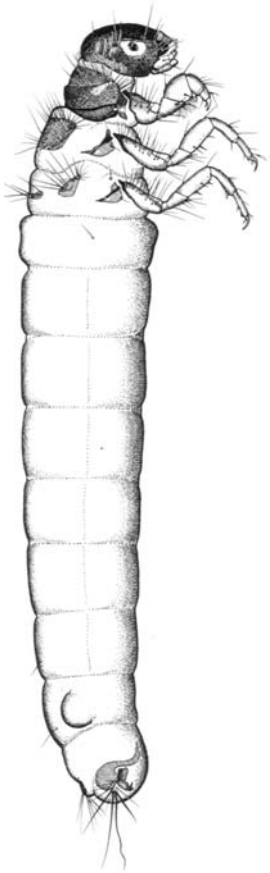


FIGURE 16.1.202 Brachycentridae, *Micrasema* habitus (lateral). *Modified from Wiggins (2004).*

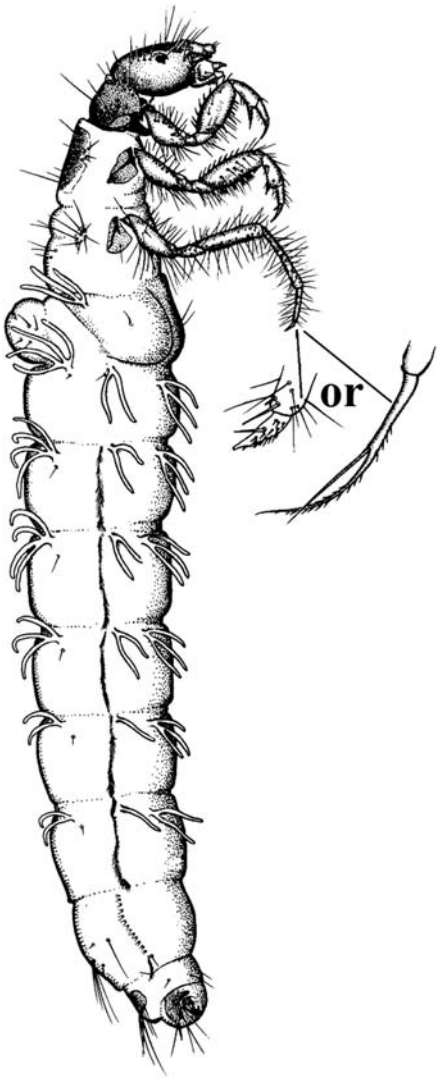


FIGURE 16.1.204 Molannidae, habitus with metathoracic claws (*Molanna* & *Molannodes*) comparison (lateral). *Modified from Wiggins (2004).*

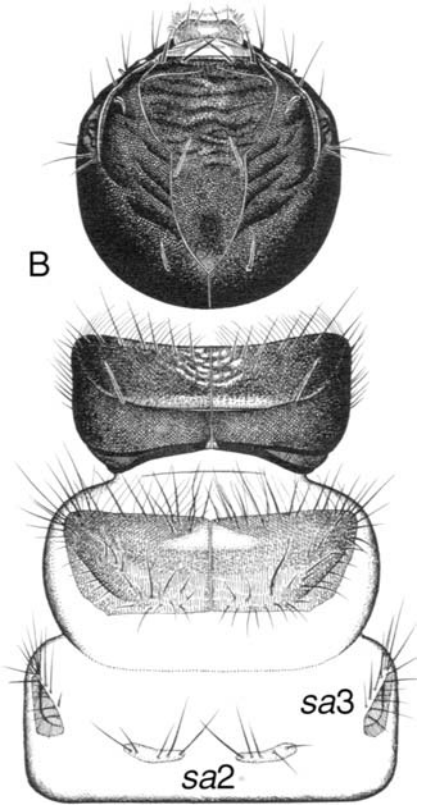


FIGURE 16.1.203 Brachycentridae, *Brachycentrus* head and thorax (dorsal). *Modified from Wiggins (2004).*

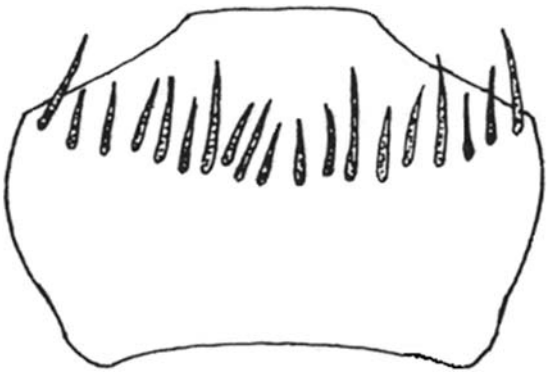


FIGURE 16.1.205 Calamoceratidae, *Heteroplecton* labrum (dorsal).

20(19) Antennae midway between eyes and base of mandibles or near base of mandibles; Ab1 dorsal hump present 21

20′ Antennae located extremely close to eyes (Fig. 16.1.192); Ab1 dorsal hump absent; case frequently four-sided, but may be round in cross-section ..... Lepidostomatidae

21(20) Antenna located near base of the mandibles 22

21′ Antennae located halfway between eyes and base of mandibles 25

22(21) Prosternal horn absent; abdominal lateral fringe absent (Beraeidae replace setae with serrate lamellae that may look like a setal fringe) 23

22′ Prosternal horn present but short; abdomen with lateral fringe; dorsal hump minute, lateral hump present; abdominal gills always single and short (Fig. 16.1.206); found in marginal pools of streams and in spring; case cylindrical of loosely spun silk with embedded plant materials—a floppy case larger than the larva ..... Phryganopsychidae, one genus: *Phryganopsyche* [Eastern Palaearctic]

23(22) Pronotum without transverse ridge and anterolateral lobe; serrate lamellae absent 24

23′ Pronotum with a transverse ridge that extends into a rounded, anterolateral lobe (Fig. 16.1.207); serrate lamellae present laterally on abdominal segments; larvae build slightly to strongly tapering sand cases in springs, seeps, and small streams ..... Beraeidae [Western Palaearctic, Japan]

24(23) Protrochantin large, hamulate (Fig. 16.1.208); anal prolegs each with about 30 long setae on dorsal surface; larval case cylindrical, tapering, of sand ..... Sericostomatidae

24′ Protrochantin small, not hamulate (Fig. 16.1.209); anal prolegs with no more than five long setae; cases of coarse sand of sturdy construction ..... Odontoceridae

25(21) Meso- and metanotum not similarly shaped; Ab1 with dorsal hump, sclerite absent; prosternal horn present; cases not tethered by long silk stalk 26

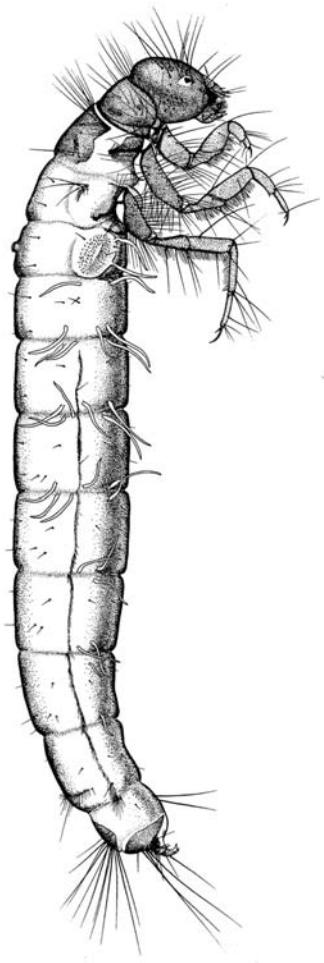


FIGURE 16.1.206 Phryganopsychidae, *Phryganopsyche* habitus (lateral). *Modified from Wiggins (2004).*

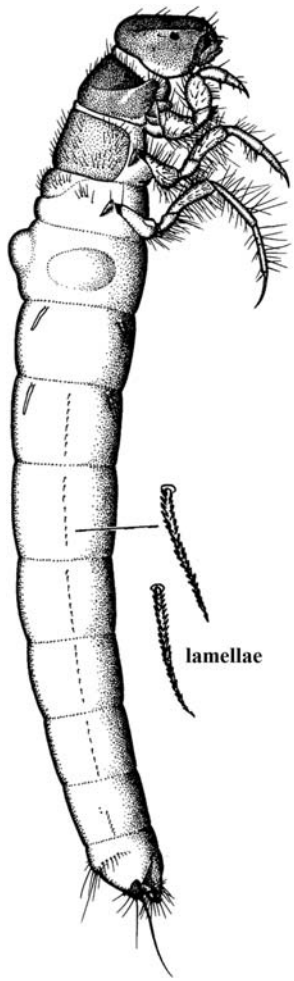


FIGURE 16.1.207 Beraeidae, *Beraea* habitus (lateral), inset serrate lamellae. *Modified from Wiggins (2004).*

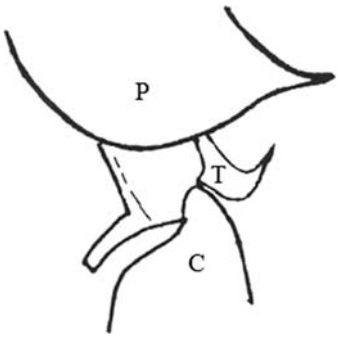


FIGURE 16.1.208 Sericostomatidae trochantin (lateral).

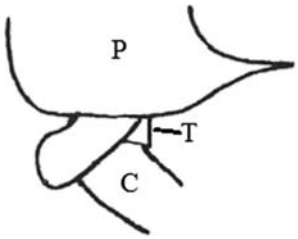


FIGURE 16.1.209 Odontoceridae, Psilotreta trochantin (lateral).

25′ Large, robust larvae with meso- and metasternum of similar shape and size (Fig. 16.1.210); prosternal horn lacking; Ab1 dorsal hump lacking but with large transverse sclerite in its place; tough silk and rock fragments produce a large case with a long silk filament cementing case to rocks in fast flowing water, surface of case with silk denticles (Fig. 16.1.211) ..... Limnocentropidae, one genus: *Limnocentropus* [Nepal to China, Japan]

26(25) Mesonotum without notch; pronotum usually wider than long; case construction again variable: tubes of leaves and bark fragments, or rock materials, or both, but of rough texture 27

26′ Mesonotum with anteromesial notch (Fig. 16.1.185); pronotum slightly longer than wide; larval cases short and of variable materials: tube of rock fragments, often with lateral ballast stones; stout sand case with slight bend; long, thin, smoothly bent sand case; or long, thin smoothly bent case of silk..... Uenoidae

27(26) Mesepisternum not enlarged anteriorly; larvae with wide range of sizes, cases of vegetative and/or mineral substrates 28

27′ Mesepisternum formed anteriorly into a prominent, elongate process (Fig. 16.1.212); medium-sized, heavy case of rock fragments, often with ballast stones (Fig. 16.1.213) ..... Goeridae

28(27) Mandibles designed for scraping of periphyton not macerating of plant material (Fig. 16.1.46) ..... Apataniidae

28′ Mandibles toothed for maceration ..... Limnephilidae

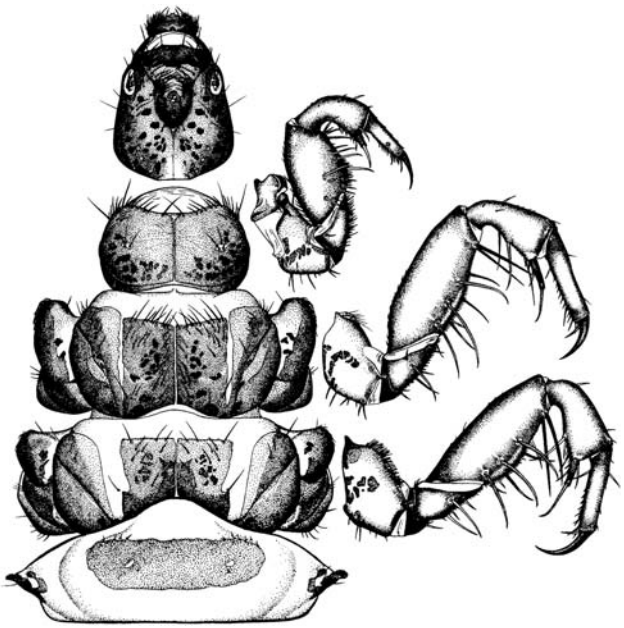


FIGURE 16.1.210 Limnocentropidae, *Limnocentropus* head and thorax (dorsal). *Modified from Wiggins (2004).*

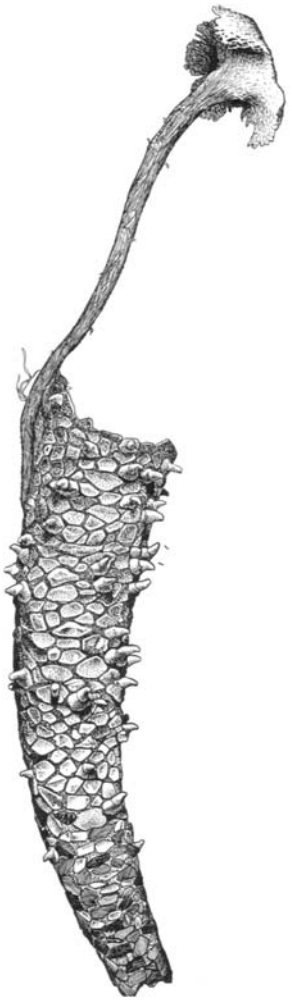


FIGURE 16.1.211 Limnocentropidae, *Limnocentropus* case (lateral). *Modified from Wiggins (2004).*

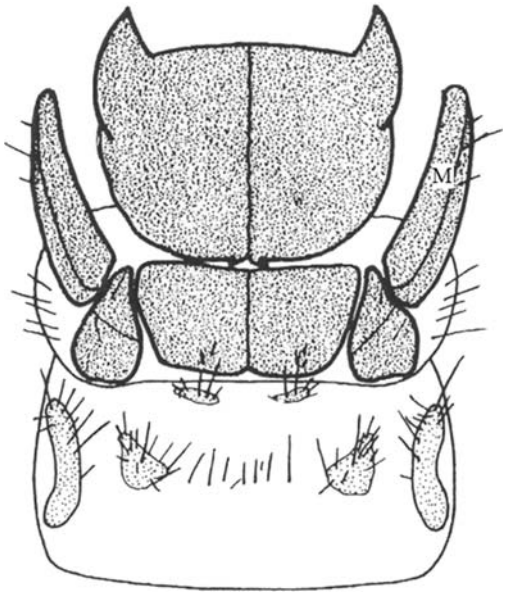


FIGURE 16.1.212 Goeridae, *Goera* thoracic nota (dorsal).

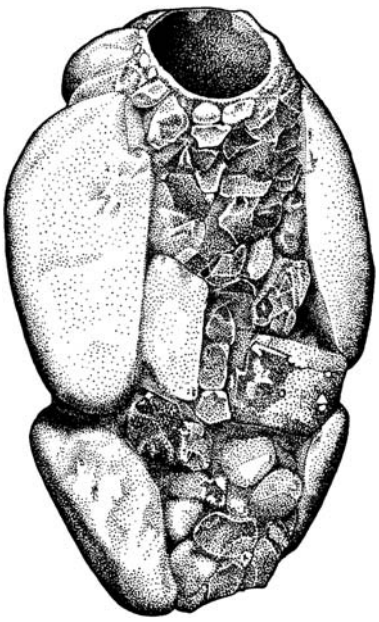


FIGURE 16.1.213 Goeridae, *Goera* case (dorsal). *Modified from Wiggins (2004).*

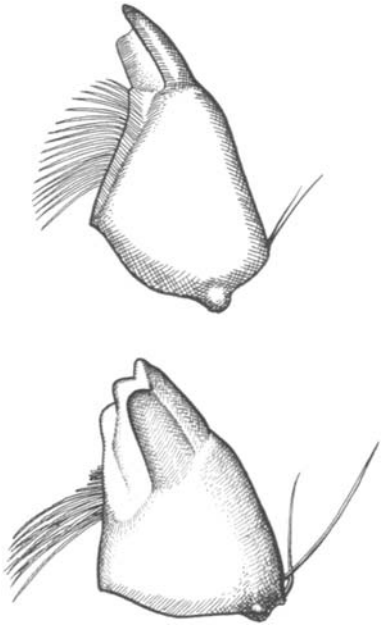


FIGURE 16.1.214 Apataniidae, mandibles (dorsal). *Modified from Wiggins (2004).*

Crustacea: Hexapoda: Insecta: Diptera: Families

This key is modified from DeWalt & Resh (2016), Courtney (1994), and Smith (1997). Diptera larvae contribute greatly to the diversity, abundance, and biomass of invertebrates in nearly every source of freshwater. The hemolymph of some dipteran families, such as the Chironomidae, contains a type of hemoglobin that colors the body red and helps with acquisition of oxygen, even from hypoxic waters. This leads to chironomids being used in domestic sewage treatment facilities as biological agents for the decay of human waste. Other Diptera utilize siphons that contain spiracles to pull atmospheric air from above the water line; therefore, presence is not governed by dissolved oxygen content of the water.

A series of review articles on the global diversity of freshwater Diptera is available and should be consulted. These include Chironomidae (Ferrington 2008), Tipuloidea (de Jong et al. 2008), Simuliidae (Currie & Adler 2008), Culicidae (Rueda 2008), and the remaining Diptera (Wagner et al. 2008).

Useful keys to Diptera larvae are found within Nilsson (1997), covering all the major families present in northern Europe and nearby. Courtney (1994) presents a key to larvae of all families and genera known in China at the time. Kawai & Tanida (2005) presented a key to the aquatic insects of Japan, in Japanese, which undoubtedly contains keys to Diptera, but this book is out of print.

We have adopted the simplified classification system used by Andersson (1997). It is still complex, and we believe a little explanation would help the reader. The suborder Brachycera of other authors is replaced with Orthorrhapha and Cyclorrhapha. A synopsis of the three suborders is presented.

- **Nematocera.** This suborder contains crane flies, gnats, mosquitos, midges, and more. Adults have at least six antennal segments. Families of these groups almost always have complete and visible head capsules and mandibles moving in a horizontal plane.
- **Orthorrhapha** (lower flies). Horse and deer flies, snipe flies, soldier flies, dance flies, and long-legged flies comprise this group. This group of flies produces no puparia, except in soldier flies. The head capsule of larvae is sclerotized dorsally, but have sclerotized rods leading posteriorly into the thorax. Mandibles move in vertical plane.
- **Cyclorrhapha** (higher flies). This suborder contains the hover flies, shore flies, dung flies, house flies, stable flies, face flies, beach flies, scuttle flies, and marsh flies. The last larval skin forms the puparium, covering the delicate, developing pupa. Larvae have the head reduced to a cephalopharyngeael skeleton, a series of skeletal rods projecting posteriorly. Mandibles move in vertical plane.

1	Mandibles move in vertical plane and parallel to each other, usually hamulate or arcuate, without secondary apical teeth and directed ventrally (Fig. 16.1.223); head capsule usually incomplete and retractile; abdomen with eight segments 2
1′	Mandibles usually moving against one another in horizontal plane, each usually with two or more apical teeth; head capsule usually complete and nonretractile (Figs. 16.1.218–220), though Tipuloidea heads are partly or completely retractile and may be reduced, but mandibles still move horizontally (Figs. 16.1.221 and 222); abdomen with at least nine segments (Nematocera) 3
2(1)	Head capsule always with distinct, even if incomplete, dorsal sclerotization; maxillae and maxillary palps distinct and usually well developed; the sclerotized rods projecting posteriorly from the head are not united; antennae well developed and arising from a sclerotized plate (Orthorrhapha) 20
2′	Head capsule not sclerotized dorsally; maxillary palps usually absent or indistinct, maxillae fused with mandibles; the sclerotized rods projecting posteriorly from head are united into a cephalopharyngeal skeleton (Fig. 16.1.262); antennae reduced or absent and, if present, situated on a membranous area (Cyclorrhapha) 25
3(1)	Head capsule partly to fully retracted within thorax, posteriorly with longitudinal incisions (Figs. 16.1.221 and 222), sometimes leaving longitudinal rods and plates; tip of abdomen with a spiracular disc consisting of from one to three pairs of short, lobes margined with setae (Fig. 16.1.224) 4
3′	Head capsule usually fully exposed, complete, without longitudinal incisions (Fig. 16.1.218); tip of abdomen without a spiracular disc bordered by lobes) 6
4(3)	Spiracular disc with ≤5 lobes 5
4′	Posterior spiracular disc with six lobes, flattened or cylindrical, sometimes reduced in size and rarely entirely sclerotized (Fig. 16.1.224) ..... Tipulidae
5(4)	Body with prominent processes, at least half as long as body width and arranged in longitudinal rows (Fig. 16.1.225) ..... Cylindrotomidae
5′	Body without prominent processes; at most with tubercles that are much shorter than half body width (Fig. 16.1.226) ..... Limoniidae or Pediciidae
6(3)	Head and thorax distinct; suctorial discs usually absent (exc. some Psychodidae) 7
6′	Body divided into six major division: cephalothorax = head + thorax + Ab1) and Ab2–6, each division with a ventral, median suctorial disc (Fig. 16.1.227) ..... Blephariceridae
7(6)	A pair of elongate, crochet tipped prolegs on Ab1 to Ab7 (Figs. 16.1.220 and 228) 8
7′	Prolegs usually absent, if present, then on no more than three abdominal segments 9
8(7)	Body compressed laterally; prolegs ventral (Fig. 16.1.228); head capsule enclosed ventrally; antennae short, simple ..... Nymphomyiidae
8′	Body compressed dorsoventrally; prolegs lateral (Fig. 16.1.220); head capsule membranous ventrally; antenna elongate, branched at apex ..... Deuterophlebiidae
9(7)	Thoracic segments indistinct, forming a single segment that is wider than any of the abdominal segments (Fig. 16.1.229) 10

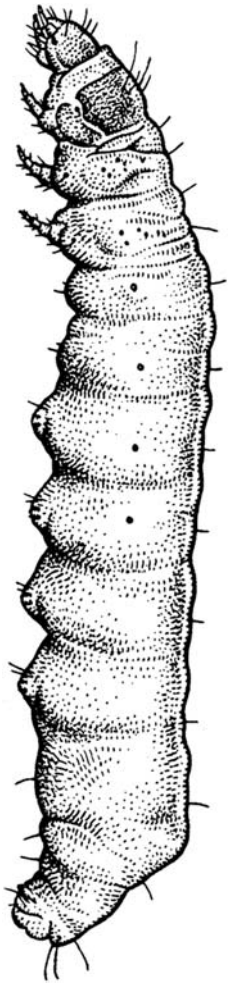


FIGURE 16.1.215 Crambidae, *Elophila* larval habitus (lateral). *Modified from Solis (2008).*

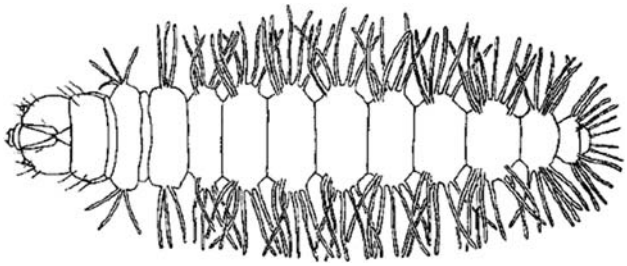


FIGURE 16.1.216 Crambidae, larva with gills (dorsal). *Modified from Solis (2008).*

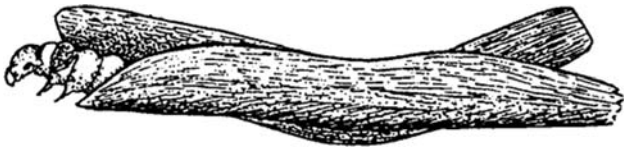


FIGURE 16.1.217 Crambidae, *Acentria ephemerella* Denis & Schiffermüller. *Modified from Agassiz (1996).*

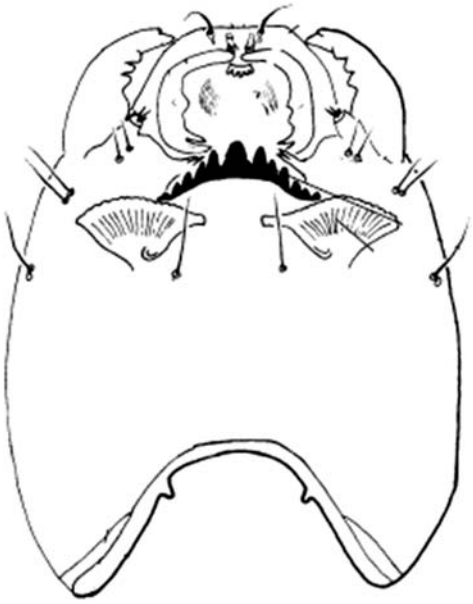


FIGURE 16.1.218 Chironomidae, Chironominae head capsule (ventral). *From Epler (2001).*

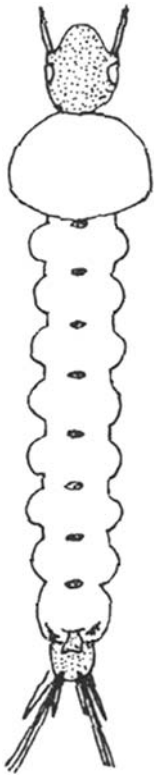


FIGURE 16.1.219 Culicidae, *Anopheles* habitus (dorsal).

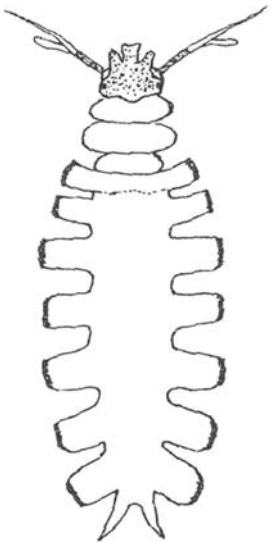


FIGURE 16.1.220 Deuterophlebiidae, *Deuterophlebia* habitus (dorsal).



FIGURE 16.1.222 Tipulidae, *Hexatoma* head (dorsal).

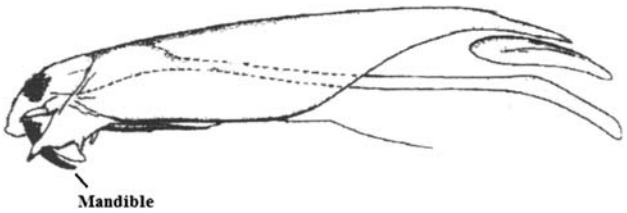


FIGURE 16.1.223 Tabanidae, *Tabanus* head (lateral).

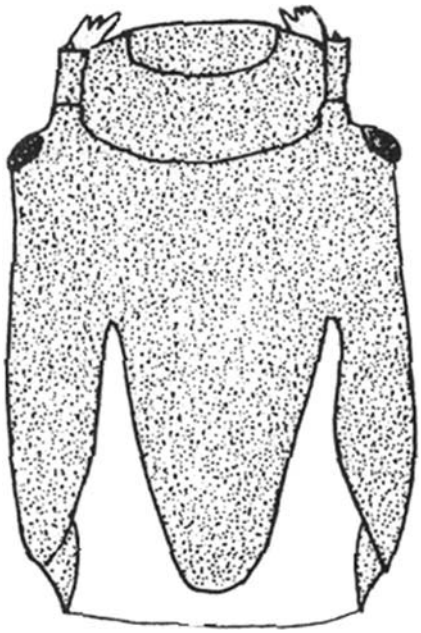


FIGURE 16.1.221 Limoniidae, *Limonia* head (dorsal).



FIGURE 16.1.224 Tipulidae, *Tipula* spiracular disc (caudal). *Modified from Smith (1997).*

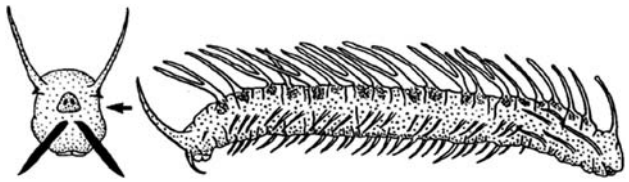


FIGURE 16.1.225 Cylindrotomidae, *Phalacrocera* habitus (lateral), inset spiracular disc (caudal). *Modified from Smith (1997).*

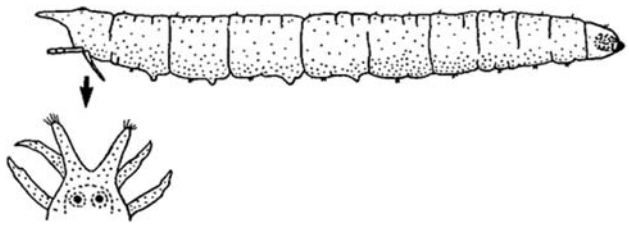


FIGURE 16.1.226 Pediciidae, *Pedicia* habitus (lateral), inset spiracular disc (dorsal). *Modified from Smith (1997).*

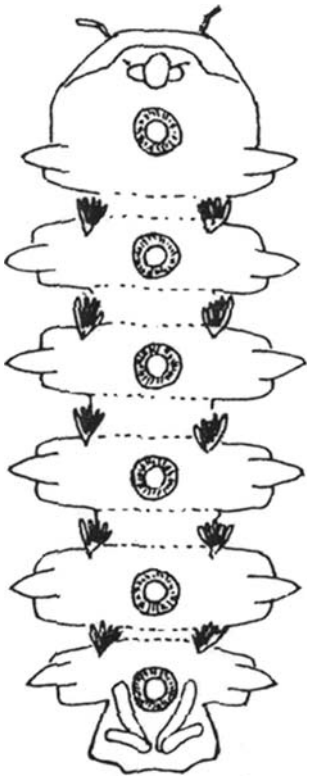


FIGURE 16.1.227 Blephariceridae, *Blepharicera* habitus (ventral).

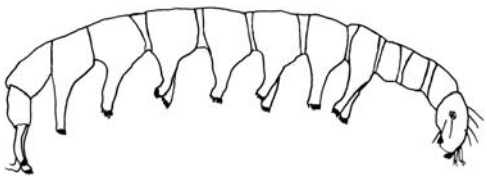


FIGURE 16.1.228 Nymphomyiidae, *Nymphomyia* habitus (lateral). *Modified from Courtney & Merritt (2008).*

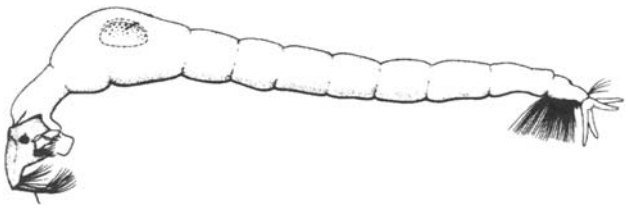


FIGURE 16.1.229 Chaoboridae, *Chaoborus* habitus (lateral). *Modified from Courtney & Merritt (2008).*

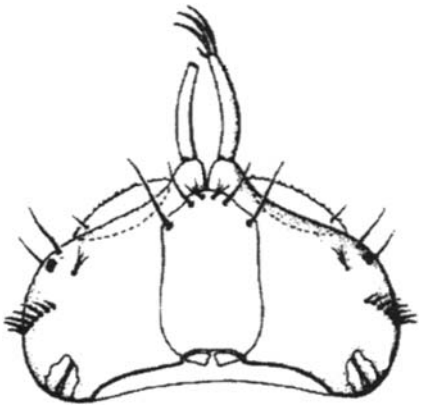


FIGURE 16.1.230 Corethellidae, Corethella head (dorsal). *Modified from Courtney & Merritt (2008).*

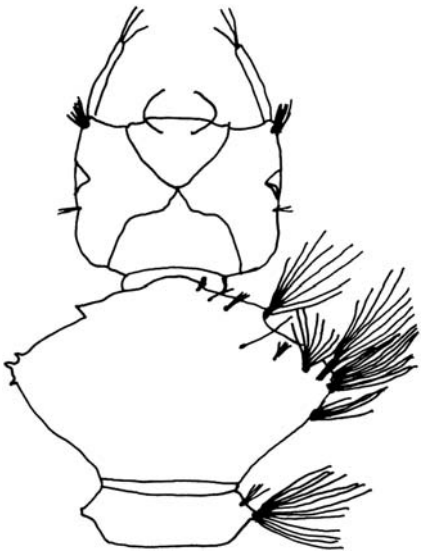


FIGURE 16.1.231 Chaoboridae, *Eucorethra* head (dorsal). *Modified from Courtney & Merritt (2008).*

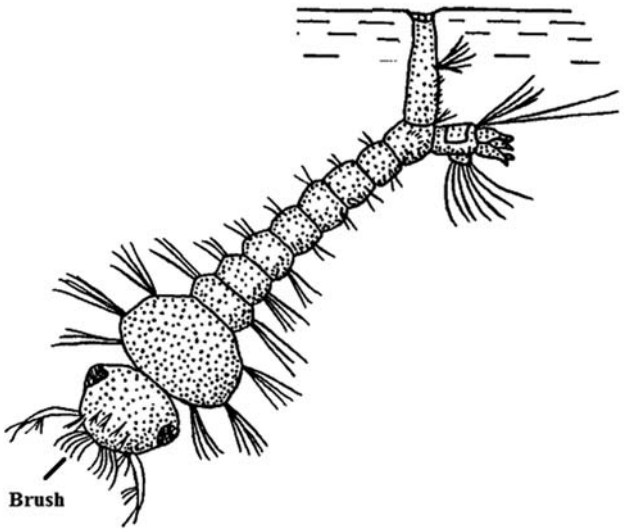


FIGURE 16.1.232 Culicidae, *Culex* habitus (lateral). *Modified from Smith (1997).*



FIGURE 16.1.233 Tanyderidae, habitus (lateral). *Modified from Courtney & Merritt (2008).*



FIGURE 16.1.234 Dixidae, *Dixa* habitus (lateral). *Modified from Courtney & Merritt (2008).*

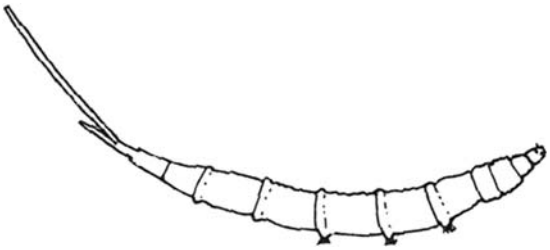


FIGURE 16.1.235 Ptycopteridae, *Ptychoptera* habitus (lateral).



FIGURE 16.1.236 Simuliidae, *Simulium* habitus (lateral).

9′	Thoracic segments usually distinguishable, about as wide as abdomen	12
10(9)	Antennae widely separated (Fig. 16.1.231); side of head without transverse row of spiniform setae; last abdominal segment with longitudinal flabelliform setal row	11
10′	Antennae close together (Fig. 16.1.230); each side of the head with transverse row of spiniform setae; last abdominal segment without ventral fan	Corethrellidae
11(10)	Antennae prehensile (grasping), with long apical setae (Fig. 16.1.229) mouth brushes absent	Chaoboridae
11′	Antennae not prehensile, with only short apical setae (Fig. 16.1.232); prominent mouth brushes on each side of labrum	Culicidae
12(9)	Prolegs with apical hooks on prothorax and/or abdomen (Figs. 16.1.233 and 234)	13
12′	Prolegs absent	19
13(12)	Prolegs on at most Ab1 to Ab3, absent from terminal segment	14
13′	Prolegs on Ab1 to Ab3 and terminal segment	15
14(13)	Abdomen terminating in long, telescopic respiratory siphon (Fig. 16.1.235); body hirsute or tuberculate; Ab1 to Ab3 with minute prolegs, each bearing a single claw	Ptychopteridae
14′	Abdomen lacking siphons; two flattened, hair-fringed lobes extending from posterior spiracles (Fig. 16.1.234); body with numerous hairs; Ab1 and usually Ab2 with crochet-tipped prolegs	Dixidae
15(13)	Prothorax ventrally with one proleg or a pair of prolegs; terminal abdominal segments lacking long filaments (Figs. 16.1.236 and 237)	16
15′	Prothorax lacking prolegs; last two abdominal segments with pairs of long filaments trailing posteriorly (Fig. 16.1.233)	Tanyderidae
16(15)	Head lacking labral fans; abdominal segments not swollen; terminal abdominal segment without ring of hooks	17
16′	Head capsule usually with pair of dorsolateral labral fans composed of long filaments; Ab5 to Ab8 swollen, giving the appearance of a bowling pin (Fig. 16.1.236); terminal abdominal segment with ring of minute hooks used to secure body to substrate	Simuliidae
17(16)	Respiratory system apneustic—no spiracles present; prothoracic or anal legs usually paired (Fig. 16.1.238)	18



FIGURE 16.1.237 Thaumaleidae, *Thaumalea* habitus (lateral). *Modified from Wagner (1997A).*

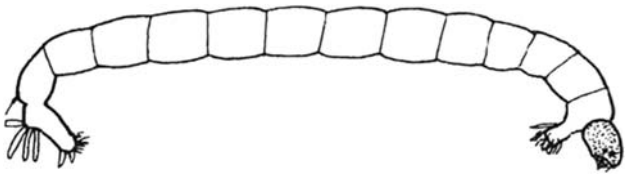


FIGURE 16.1.238 Chironomidae, Chironomus habitus (lateral).

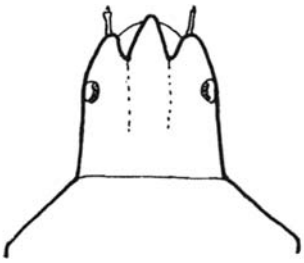


FIGURE 16.1.243 Stratiomyidae, *Odontomyia* head (dorsal).

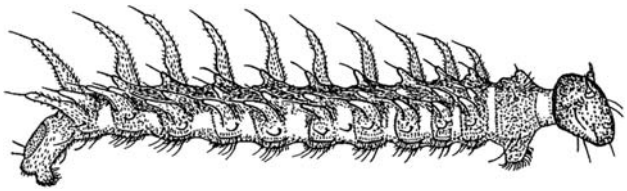


FIGURE 16.1.239 Ceratopogonidae, *Atrichopogon* habitus (lateral). *Modified from Smith (1997).*

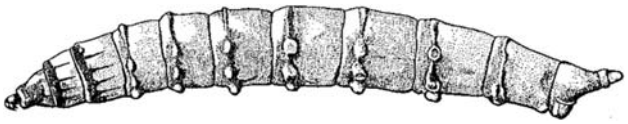


FIGURE 16.1.244 Tabanidae, *Tabanus* habitus (lateral). *Modified from Smith (1997).*

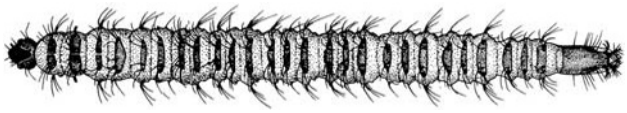


FIGURE 16.1.240 Psychodidae, *Pericoma* habitus (dorsal). *Modified from Wagner (1997B).*

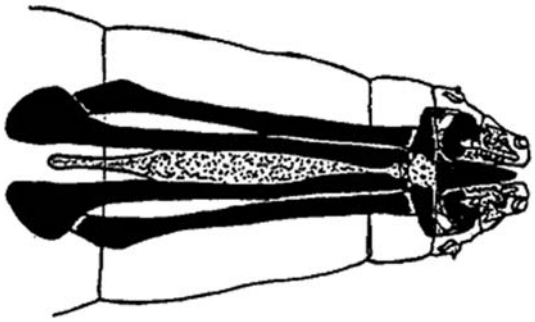


FIGURE 16.1.245 Dolichopodidae, *Hydrophorus* mouthparts (dorsal). *Modified from Smith (1997).*

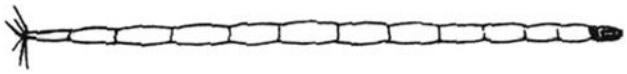


FIGURE 16.1.241 Ceratopogonidae, *Palpomyia* habitus (lateral).



FIGURE 16.1.246 Pelocorynchidae, *Glutops* habitus (lateral). *Modified from Thomas (1997).*

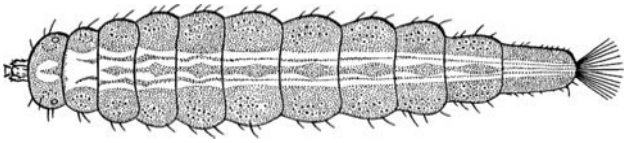


FIGURE 16.1.242 Stratiomyidae, *Odontomyia* habitus (dorsal). *Modified from Smith (1997).*

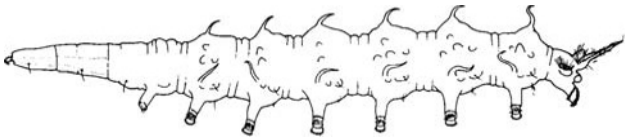


FIGURE 16.1.247 Athericidae, *Ibisia* habitus (lateral). *Modified from Thomas (1997).*

17′	Respiratory system amphineustic with anterior spiracles on a short stalk and posterior ones in a transverse cleft on Ab8; body smooth, without prominent setae but with dark, sclerotized dorsal saddles; prothoracic and anal prolegs unpaired (Fig. 16.1.237); found on rocks and mosses in shallow water film (hygropetric habitats) ..... Thaumaleidae
18(17)	All body segments with prominent dorsal tubercles and/or setae (Fig. 16.1.239) ..... Ceratopogonidae (In part)
18′	Body segments lacking prominent tubercles and setae (Fig. 16.1.238) ..... Chironomidae
19(12)	Body segments secondarily divided into two or three subdivisions, often indicated by narrow, transverse sclerotized plates (Fig. 16.1.240); respiratory system amphineustic, posterior spiracles usually at apex of short conical siphon ..... Psychodidae
19′	Body segments usually not secondarily divided, integument smooth, shiny, without sclerotized plates or other surface features; respiratory system apneustic (Fig. 16.1.241) ..... Ceratopogonidae (In part)
20(2)	Body not conspicuously compressed; integument sometimes leathery, but not toughened or faceted; head extends and retracts into thorax freely 21
20′	Body dorsoventrally compressed (Fig. 16.1.242); integument with calcareous deposits forming reticulate facets; head permanently exposed and nearly immovable (Fig. 16.1.243) ..... Stratiomyidae
21(20)	Head well developed dorsally, closed ventrally by a submental plate (Fig. 16.1.223); tentorial arms fused with anterior sclerites of head capsule; a brush of backwardly curved spines usually present above and near base of each mandible 22
21′	Head reduced to pair of metacephalic rods (Fig. 16.1.245); metacephalic rods and tentorial arms flexibly articulate with sclerites of head; spines near mandible absent 24
22(21)	Posterior spiracles absent or within small terminal cavity; abdomen without welts or prolegs (Fig. 16.1.246) or with one pair of ventral prolegs on each segment, long filaments may be present on last abdominal segments (Figs. 16.1.247 and 248) 23
22′	Terminal fissure vertical; head capsule not strongly sclerotized, retractile within thorax, body cylindrical; Ab1 to Ab7 encircled by three or four pairs of fleshy welts or prolegs, each sometimes bearing apical spines (Fig. 16.1.244) ..... Tabanidae
23(22)	Abdominal segments each with pair of ventral prolegs bearing hooks; slender tubercles of progressively increasing size laterally and dorsally on Ab1 through Ab7 (Figs. 16.1.247 and 248) ..... Athericidae
23′	Abdominal segments without prolegs or tubercles; segmentation beadlike (Fig. 16.1.246) ..... Pelecorhynchidae

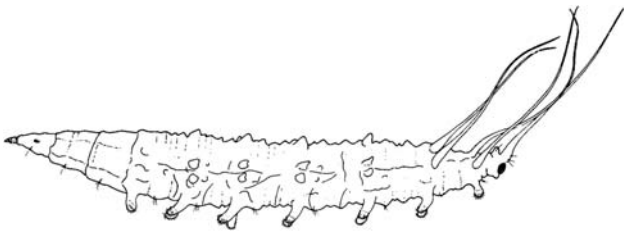


FIGURE 16.1.248 Athericidae, *Atrichops* habitus (lateral). *Modified from Thomas (1997).*

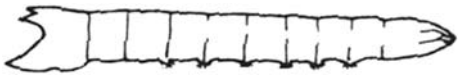


FIGURE 16.1.249 Dolichopodidae, habitus (lateral).

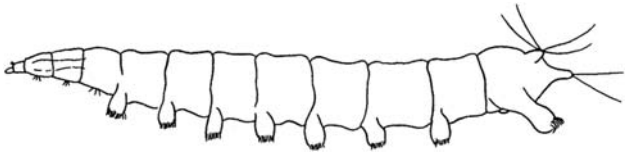


FIGURE 16.1.250 Empididae, *Clinocera* habitus (lateral). *Modified from Smith (1997).*

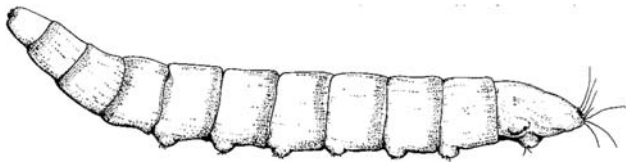


FIGURE 16.1.251 Empididae, *Chelifera* habitus (lateral). *Modified from Wagner (1997C).*

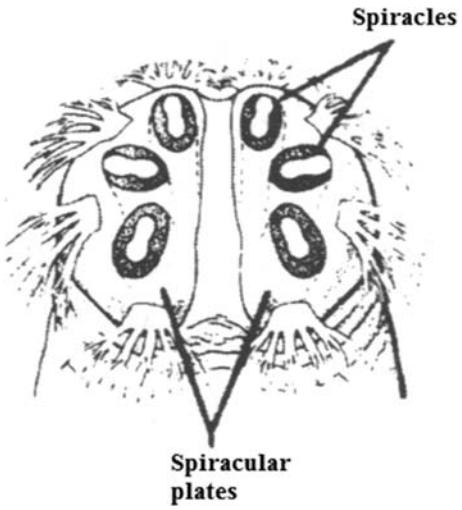


FIGURE 16.1.252 Canacidae, *Canace* spiracular plates (caudal). *Modified from Courtney & Merritt (2008).*

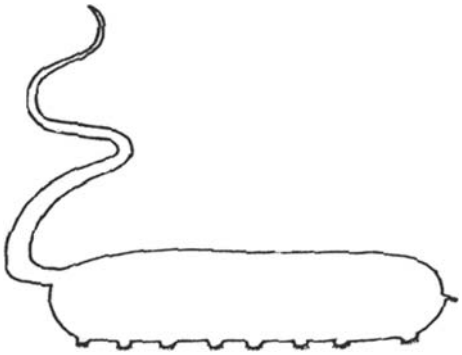


FIGURE 16.1.253 Syrphidae, *Eristalis* habitus (lateral).

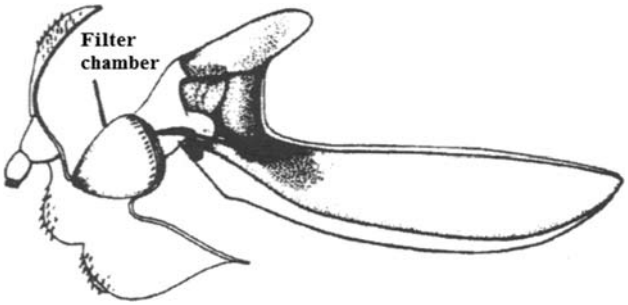


FIGURE 16.1.257 Syrphidae, *Eristalis* mouthparts. *Modified from Courtney & Merritt (2008).*

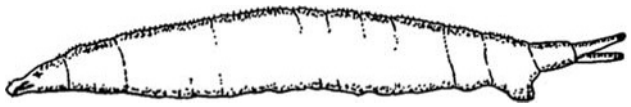


FIGURE 16.1.254 Ephydridae, *Scatella* habitus (lateral). *Modified from Smith (1997).*

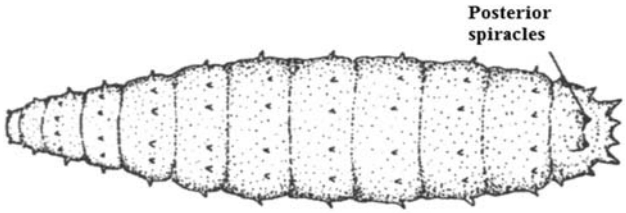


FIGURE 16.1.258 Phoridae, habitus (dorsal). *Modified from Courtney & Merritt (2008).*

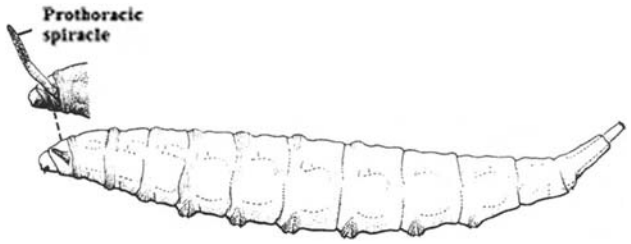


FIGURE 16.1.255 Canacidae, *Canace* habitus (lateral), inset head with anterior spiracle location. *Modified from Courtney & Merritt (2008).*

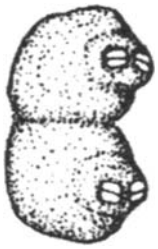


FIGURE 16.1.259 Phoridae, posterior spiracles atop papillae (dorsal). *Modified from Courtney & Merritt (2008).*

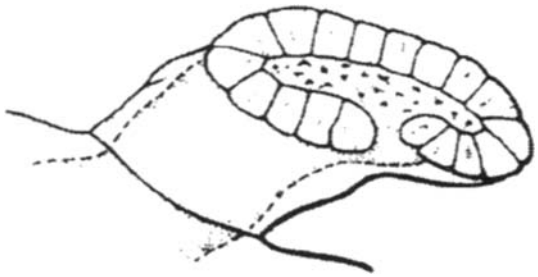


FIGURE 16.1.256 Syrphidae, *Eristalis* anterior spiracle (dorsal). *Modified from Courtney & Merritt (2008).*

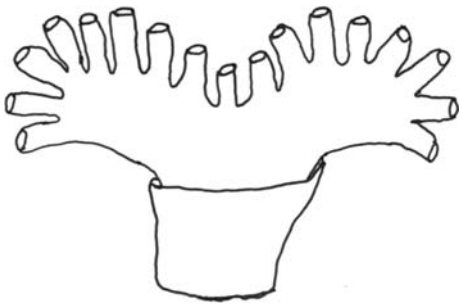


FIGURE 16.1.260 Scathophagidae, anterior spiracles. *Redrawn from Courtney & Merritt (2008).*



FIGURE 16.1.261 Sciomyzidae, *Sepedon* habitus (dorsal). *Modified from Courtney & Merritt (2008).*



FIGURE 16.1.262 Sciomyzidae, *Sepedon* head (lateral) and inset of ventral arch (ventral). *Modified from Courtney & Merritt (2008).*

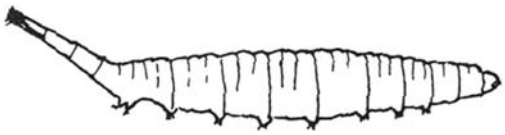


FIGURE 16.1.263 Ephydridae, habitus (lateral).

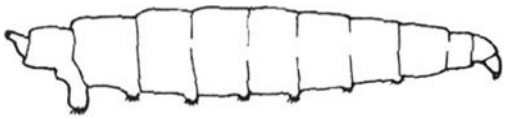


FIGURE 16.1.264 Muscidae, *Limnophora* habitus (lateral).

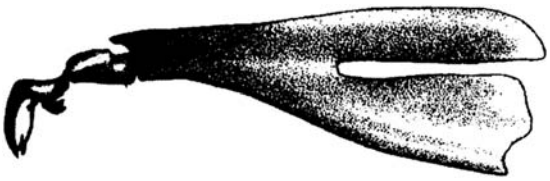


FIGURE 16.1.265 Muscidae, *Limnophora* accessory mouth sclerites (lateral). *Modified from Courtney & Merritt (2008).*

24(21)	Larvae metapneustic; terminal abdominal segment with four (rarely two) primary lobes surrounding spiracles; transverse ventral creeping welts on abdominal segments (Fig. 16.1.249); metacephalic rods expanded posteriorly (Fig. 16.1.245) ..... Dolichopodidae
24′	Larvae usually apneustic, terminal abdominal segment with one to four rounded lobes bearing apical setae, and abdominal segments with paired prolegs bearing apical hooks (Fig. 16.1.250); or if metapneustic, terminal segment with a single lobe beneath spiracles, and abdominal segments with ventral creeping welts (Fig. 16.1.251); metacephalic rods slender posteriorly ..... Empididae
25(2)	Posterior spiracular plates fused or closely appressed (Fig. 16.1.252), usually at apex of telescopic siphon (Fig. 16.1.253) 26
25′	Posterior spiracular plates distinctly separated (Fig. 16.1.254), may or may not be at apex of telescopic siphon 27
26(25)	Anterior spiracles with openings on a branched papilla, or arranged along apical half of a long spiracular stalk (Fig. 16.1.255); cephalopharyngeal skeleton with well-developed mouth hooks ..... Canacidae
26′	Anterior spiracles, if present, with openings near apex of simple stalk (Fig. 16.1.256); cephalopharygeal skeleton without mouth hooks, replaced by ribbed filter chamber (Fig. 16.1.257); some with long respiratory siphons (Fig. 16.1.253) ..... Syrphidae
27(25)	Anterior spiracles either absent or bearing two or more short or branched papillae (Fig. 16.1.260); posterior spiracles with openings usually arranged in parallel or in radiating pattern 28
27′	Anterior spiracles simple, each with one to several openings arranged peripherally at apex of short projection; body often dorsoventrally flattened and bearing a series of spicules or tubercles (Fig. 16.1.258); posterior spiracles on dorsal surface arranged atop two papillae (Fig. 16.1.259) ..... Phoridae
28(27)	Body variable, if covered with short, fine hairs, then a respiratory siphon present, or each spiracle on a short tubular projection on terminal segment; cephalopharyngeal skeleton without a ventral arch 29
28′	Body segments often covered with short, fine hairs; last segment often tapered, with tubercles surrounding spiracles that are only slightly elevated (Fig. 16.1.261); cephalopharyngeal skeleton with a sclerotized, anteriorly serrated, ventral arch below base of mouth hooks (Fig. 16.1.262) ..... Sciomyzidae
29(28)	Last abdominal segment rather truncate, and/or with setae on only intersegmental areas; tubercles, if present, on only last abdominal segment 30
29′	Last abdominal segment somewhat tapered, sometimes ending in a retractable respiratory siphon (Figs. 16.1.254 and 263); posterior abdominal segments covered with setae, spines, or setose tubercles ..... Ephydridae
30(29)	Posterior spiracular openings radiating from ecdysial scar at distinctly less than right angles, or irregularly arranged; prothoracic spiracle a sieve-like plate or with >10 papillae arranged in a bilobed fan (Fig. 16.1.260) ..... Scathophagidae
30′	Posterior abdominal segment without tubercles surrounding spiracles (Fig. 16.1.264); anterior spiracles, if present, fan-shaped, and usually with fewer than 10 papillae; accessory oral sclerite below mouth hooks (Fig. 16.1.265) ..... Muscidae

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Chapter 16.2

Arthropoda: Class Branchiopoda

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INTRODUCTION

Approximately 400 species of branchiopod crustaceans are found in Palaearctic temporary and permanent aquatic habitats, from small seasonal wetlands to lakes, ponds, and large rivers. Most are planktonic or semi-benthic and are often among the most abundant invertebrates in those habitats. Branchiopods are often used as indicators of aquatic ecosystem health, which ultimately reflects on land-use practices and management (Rogers, 2009). Several species are protected by environmental laws, and some species are economically important.

LIMITATIONS

The Palaearctic anostracans are well known in Europe and North Africa. New species are still being discovered in Asia every year. The anostracan keys presented here are based primarily on male characters, but females can be identified for some taxa. There are around 110 Palaearctic species (Brendonck et al., 2008) to date. The notostracans are represented by two genera: *Lepidurus* and *Triops*, both in need of revision. Laevicaudatan clam shrimp are easily identified. The spinicaudatan clam shrimp are more difficult to identify; most genera need revision, and the species of *Eulimnadia* require specimens with mature eggs for identification.

The anostracan genus *Chirocephalus* needs to be revised. New species are discovered every few years, but many older species may not be valid.

In Europe and Asia, there are a few species that are protected under federal laws and most Palaearctic countries require collecting and export permits.

Cladocera keys are primarily based upon adult females, which are readily identified to genus. Species-level identifications typically require use of a compound microscope, and many genera need to be revised or have incompletely known species.

TERMINOLOGY AND MORPHOLOGY

Palaearctic branchiopods range in size from <1 mm to 10 cm. Adult branchiopods retain the reduced first antennae of the larvae. In notostracans and laevicaudatans the second antennae are greatly reduced. Diplostracan second antennae are typically branched, with anterior and posterior rami, and are used for propulsion. The anostracan second antenna is made of two **antennomeres** (proximal and distal). Anostracan second antennae are robust, and in males may have prehensile or cheliform antennal appendages (sometimes fused medially into a central cephalic appendage), posteriolateral basal projections called **apophyses**, and/or anteriomedial spiny patches called **pulvilli** (singular: pulvillus). In *Streptocephalus* the antennal appendages are cheliform, divided into two rami, referred to as a **thumb** and **finger** (Fig. 16.2.1 I). The thumb is typically longer than the finger and may have a posterior spur. The finger may have one or more **teeth** on the anterior margin.

The head is proportioned to the body in anostracans, notostracans, and spinicaudatans, but is massive in the laevicaudatans and may be larger than the rest of the animal. A **rostrum** is absent in anostracans and notostracans.

The nauplii have a single median eye, which is reduced in most adult large branchiopods, but in the Notostraca becomes a large tubercle on the **nuchal organ**, behind the eyes. The adult compound eyes are fused in laevicaudatans and diplostracans, but are separate and borne on stalks in anostracans. In Cladocera, the naupliar eye may be posterior to the compound eye, and some cave-dwelling cladocerans lack eyes entirely. The nuchal organ lies on the dorsal surface of the head; although in the spinicaudatan family Limnadiidae, it is borne on a short stalk.

Palaearctic anostracans have 11 pairs of thoracopods (17 in *Polyartemiella*, 19 in *Polyartemia*).

Cladoceran sexes are morphologically similar, with small differences in appendages and body shape. Because most cladocerans reproduce asexually at least part of the time, most individuals will be females.

MATERIAL PREPARATION AND PRESERVATION

All branchiopods can be preserved in ethyl alcohol long term, and for purposes of identification all can be manipulated in alcohol. Dissection is seldom necessary, but it is a good idea to have several animals available for identification, especially for cladocerans because these small, delicate animals are easily crushed. Cladocerans smaller than about 1 mm should be slide-mounted for high-magnification viewing. Larger species can often be identified without being mounted, using a dissecting microscope at about 50 diameters magnification or less. The best cladoceran mounting medium is one which is more or less permanent and soluble in both water and alcohol solutions so specimens can be added directly to the medium without tedious dehydration. If you have access to chloral hydrate (currently a controlled substance), a good medium is Hoyer's:

Dissolve 30 g of ground gum Arabic in 170 mL of hot distilled water. Add 200 g of chloral hydrate and 20 g of glycerine.

Divide the Hoyer's into two batches. Let one sit in a warm place until it is as thick as honey, and keep the second batch in a closed jar so it remains thin. You can always add more water to thin either batch. Keep at least some of the thick and thin Hoyer's in screw-top eye-dropper bottles.

To make a slide, use the eye dropper to put a small streak of dilute Hoyer's (about a quarter of a drop) toward one end of the slide. Arrange the specimens in this streak. It is wise to place four or so of what you think are the same kind of animal on a slide to allow for comparison and viewing of difficult characteristics. Delicate specimens can be protected from compression by putting a few pieces of broken coverslips around the specimens. Let the Hoyer's streak dry on a slide warmer or in a warm place (below 100°C). When the streak is dry, add a drop or two of the thick Hoyer's and gently lower a cover glass over the Hoyer's. Put the slide back into a warm place to dry again. Label the slide as to the date and location of the collection. It is important to use thickened Hoyer's in the last step; otherwise, the Hoyer's will shrink as it dries and produce large bubbles in the final preparation. However, if you use thickened Hoyer's, small bubbles produced will disappear as the medium dries. These slides are semipermanent. If the climate is humid, the Hoyer's will thin and cover glasses will slip off the slide. If the climate is arid, the Hoyer's will desiccate enough so that the cover glasses pop off the slide. These problems may be avoided by storing the slides horizontally in a climate that has moderate humidity, and by ringing the slide with clear nail polish.

An alternate mounting method, especially useful for bosminids, chydorids, and macrothricids, is to use polyvinyl lactophenol stained with lignin pink. Temporary slides can be made using glycerol or glycerine jelly. Best of all for museum specimens is possibly Canada Balsam, although this requires the specimens be dehydrated through an alcohol series.

KEYS TO BRANCHIOPODA

The cladoceran keys were supported in part by the Russian Science Foundation (grant 14-14-00778).

Branchiopoda: Orders

1	Compound eyes sessile; carapace present or absent (Figs. 16.2.1 B–F, K–M) 2
1′	Compound eyes on stalks separated; carapace absent (Fig. 16.2.1 A) ..... **Anostraca [p. 646]**
2(1)	Carapace bivalved, folded or reduced; eyes not projecting dorsally through carapace (Figs. 16.2.1 C–F, K–M) ... **Diplostraca [p. 663]**
2′	Carapace broad, never folded or bivalved; eyes projected dorsally through carapace (Fig. 16.2.1 B) ..... Notostraca, one family: **Triopsidae [p. 661]**

Branchiopoda: Anostraca: Families

1	Praeepipodites not cleft or divided (Fig. 16.2.1 H) 2
1′	Praeepipodites (Fig. 16.2.1 G) obviously cleft, or entirely divided in two ..... **Chirocephalidae [p. 646]**
2(1)	Second antennal distal antennomere not broadly triangular; brood pouch without large pair of spines (Figs. 16.2.1 I, N) 3
2′	Second antennal distal antennomere broadly triangular, apex acute (Fig. 16.2.1 J); brood pouch with a ventral pair of large, recurved spines, halophiles, widespread ..... Artemiidae, one genus: ***Artemia*** **[p. 655]**
3(2)	Gonopod rigid basal portions parallel, directed ventrally, with the bases closely united (Fig. 16.2.2 A); male antennal and/or frontal appendages present or not; female second antennae lamellar, 2–3 times as broad as thick 4
3′	Gonopods directed ventrolaterally, widely separated at the base (Fig. 16.2.2 B); male frontal and antennal appendages always absent, although rigid projections may be present; female second antennae subcylindrical in cross-section; widespread (Fig. 16.2.1 N) ..... Branchinectidae, one genus: ***Branchinecta*** **[p. 655]**
4(3)	Male second antennal proximal antennomere with or without appendages, if present, then appendages cylindrical or lamellar, but never cheliform; second antennae and appendages not laterally compressed 5
4′	Male second antennal proximal antennomere terminating in a large, cheliform, multiramal appendage directed ventrally (Fig. 16.2.1 I); second antennae and appendages laterally compressed; widespread ..... Streptocephalidae, one genus: ***Streptocephalus*** **[p. 656]**
5(4)	Male second antennae with proximal antennomeres fused together into a rigid clypeus; clypeus soft proximally, and chitinized distally; vas deferens always without a dorsal loop 6
5′	Male second antennae with proximal antennomeres fused basomedially, or medially coalescent, distal portions always free (Fig. 16.2.2 D); vas deferens always with a dorsal loop (usually visible through the integument) ..... **Thamnocephalidae [p. 658]**
6(5)	Rigid portion of gonopod with a basoventral, lamellar, subtriangular projection, with one or more spines along medial margin, shorter than apical spine; greatest width of eversible portion of gonopod 0.5–1.2 x length; gonopod with one short, medial row of spines ending about one third the length of the gonopod from the apex (Fig. 16.2.2 A) ..... **Tanymastigidae [p. 658]**
6′	Rigid portion of gonopod without a basomedial projection, or if projection is present, then bearing one spine, shorter than the apical spine, on the lateral margin; greatest width of eversible portion of gonopod ≤0.25x length; gonopod with one or more longitudinal rows of spines (Fig. 16.2.2 C) ..... **Branchipodidae [p. 660]**

Branchiopoda: Anostraca: Chirocephalidae: Genera

1	More than 17 pairs of thoracopods, abdomen reduced, much shorter than thorax; male second antennal antennomeres fused and branched (Figs. 16.2.1 A and 16.2.2 E, F) 2
1′	Eleven pairs of thoracopods; abdomen nearly as long as thorax or longer 3
2(1)	Seventeen pairs of thoracopods (Fig. 16.2.1 A); male head as in Fig. 16.2.2 E ..... *Polyartemiella hazeni* (Murdoch, 1884) [Arctic Beringia]
2′	Nineteen pairs of thoracopods; male head as in Fig. 16.2.2 F ..... *Polyartemia forcipata* Fischer, 1851 [Arctic]
3(1)	Male second antennal distal antennomere with a medial spine; antennal appendage absent OR not reaching second antenna distal antennomere (Fig. 16.2.2 G) 4
3′	Male second antennal distal antennomere without a medial spine situated equidistant between distal and proximal ends, OR, if one spine present, then antennal appendage longer than second antenna proximal antennomere (Figs. 16.2.2 H, M–N and 16.2.3 A) 5

4(3) Male second antennal distal antennomere with a single medial spine directed medially; antennal appendage lobiform, short (Fig. 16.2.2 G) ..... *Pararteмiopsis longicornis* (Smirnov, 1930) [Central Asia]

4′ Male second antenna distal antennomere with two medial spines; proximal antennomere without a lamellar or triangular appendage; brood pouch transverse, about twice as broad as long (Fig. 16.2.2 H) ..... *Artemiopsis* **[p. 647]**

5(3) Cercopods articulating at base, lateral and medial margins edged in plumose setae; male second antennal proximal antennomere with anteriobasal appendages; everted portion of gonopod subcylindrical to spiniform 6

5′ Cercopods not articulating, rigid, short with a few ventrolateral separated setae; male second antennal proximal antennomere without anteriobasal appendages; everted portion of gonopods a broad, flattened process with distal margin crenulate (Fig. 16.2.2 J) ..... *Branchinectella media* (Schmankewitsch, 1873) [Halophile; Mediterranean region, central Asia]

6(5) Second antennal appendage 0.5−2.5 times as long as the proximal antennomere (Fig. 16.2.3 A) 7

6′ Second antennal appendage less than 0.5 times as long as the proximal antennomere (Figs. 16.2.2 M, N) ..... ***Linderiella*** **[p. 647]**

7(6) Everted portion of gonopod spiniform, chitinized, recurved, apically acute, with denticles on concave side (Fig. 16.2.3 B) ..... ***Eubranchipus*** **[p. 647]**

5′ Everted portion of gonopod conical, not chitinized, without denticles (Fig. 16.2.3 C) ..... ***Chirocephalus*** **[p. 651]**

Branchiopoda: Anostraca: Chirocephalidae: *Artemiopsis*: Species

1 Male second antenna, proximal antennomere with a single, small medial conical projection; second antenna distal antennomere with apex curving slightly medially (Fig. 16.2.2 H) ..... *Artemiopsis bungei* Sars, 1897 [Russia. Nearctic]

1′ Male second antenna, proximal antennomere without a medial projection; second antenna distal antennomere with apex bent medially 90° from antennomere axis (Fig. 16.2.2 I) ..... *Artemiopsis plovmornini* Jaschinov, 1925 [Russia]

Branchiopoda: Anostraca: Chirocephalidae: *Linderiella*: Species

1 Male antennal appendage apex pedunculate and asymmetrical, projecting distally (Figs. 16.2.2 L, M) 2

1′ Male antennal appendage pedunculate, symmetrical (Fig. 16.2.2 K) ..... *Linderiella africana* Thiéry, 1986 [Morocco]

2(1) Male second antenna, distal antennomere arcing in proximal third 3

2′ Male second antenna, distal antennomere arcing in distal third; antennal appendage distal projection long, tapering, without apical spines ..... *Linderiella jebalae* Boix, Sala, & Alonso, 2016 [Morocco]

3(2) Egg spines distally expanded ..... *Linderiella baetica* Alonso & Garcia-de-Lomas, 2009 [Spain]

3′ Egg spines acute ..... *Linderiella massaliensis* Thiéry & Champeau, 1988 [France]

Branchiopoda: Anostraca: Chirocephalidae: *Eubranchipus*: Species

1 Male lacking a broad, cornified labral projection (Fig. 16.2.3 A) 2

1′ Male with a broad, cornified labral projection (Figs. 16.2.3 D, H, I) 4

2(1) Antennal appendage broad, with lateral margin bearing long digitiform papillae; second antenna distal antennomere lacking a lobiform basomedial projection half as long as the antennomere (Fig. 16.2.3 A) 3

2′ Antennal appendage narrow, tapering; margin with spiniform papillae; second antenna distal antennomere with a broad, lobiform basomedial projection at least one half the length of the antennomere (Fig. 16.2.3 E) ..... *Eubranchipus* (*Drepanosurus*) *vladimiri* Vekhoff & Vekhova, 1992 [Russia]

3(2) Second antenna distal antennomere with a small anteriobasal projection bearing spines, that extend distally along a ridge toward the apex (Fig. 16.2.3 G); apophyses lobiform, constricted at base ..... *Eubranchipus* (*Drepanosurus*) *claviger* (Fischer, 1851) [Russia]

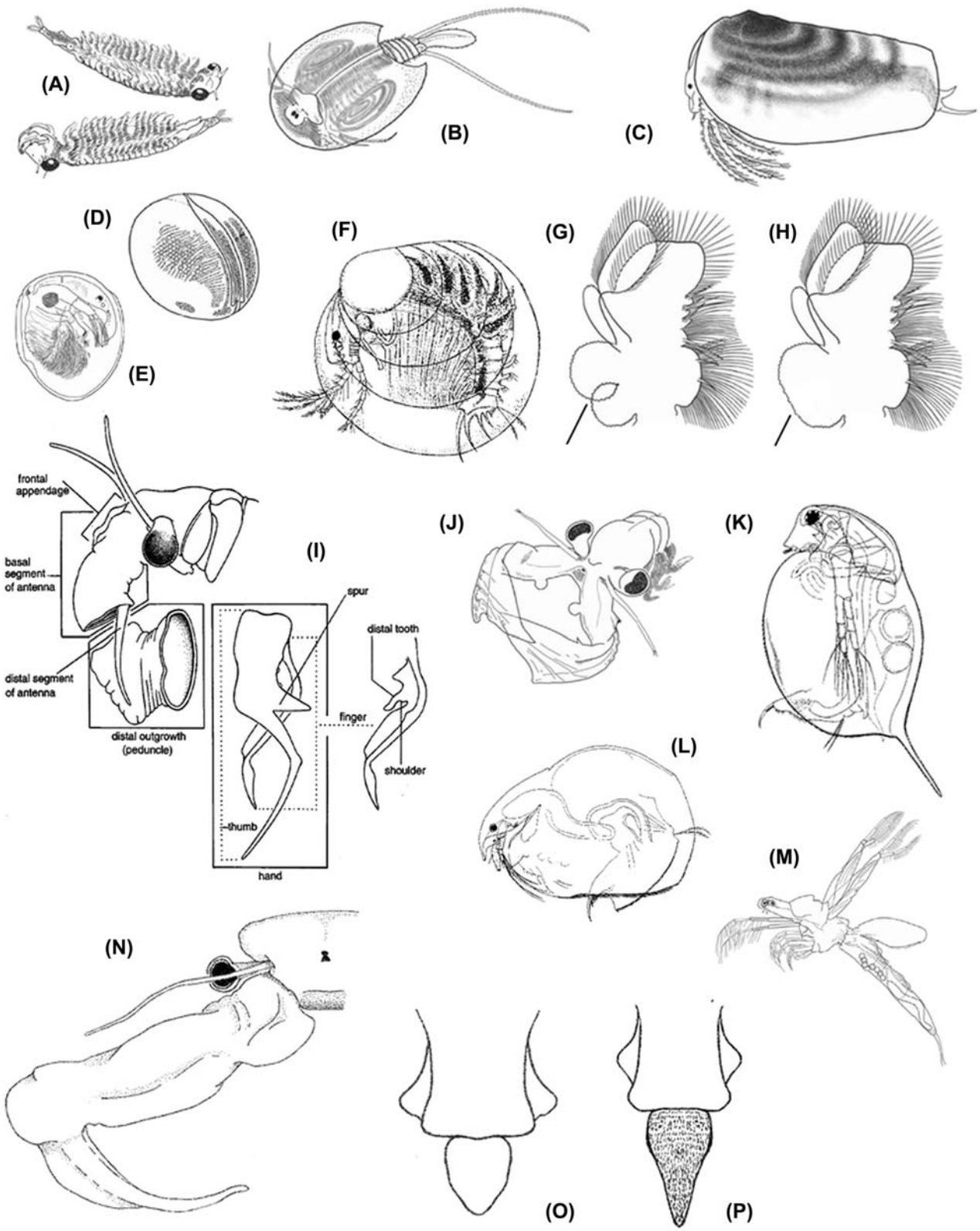


FIGURE 16.2.1 (A) *Polyartemiella hazeni* habitus (upper female, lower male); (B) *Triops* sp. habitus; (C) *Leptestheria* habitus; (D) *Lynceus bracyurus* habitus; (E) *Lynceus brachyurus*, right lateral view, right carapace half removed; (F) *Cyclestheria* sp. habitus; (G) *Eubranchipus* sp. left thoracopod V, anterior view; (H) *Branchinecta* sp. left thoracopod V, anterior view; (I) *Streptocephalus* sp. generalized, exploded view; (J) *Artemia franciscana* male head; (K) *Daphnia* sp; (L) Eurycercidae; (M) *Leptodora* sp; (N) *Branchinecta ferox*, male head left half, anterior view; (O) *Branchinecta ferox*, labrum, ventral view; (P) *Branchinecta orientalis*, labrum ventral view.

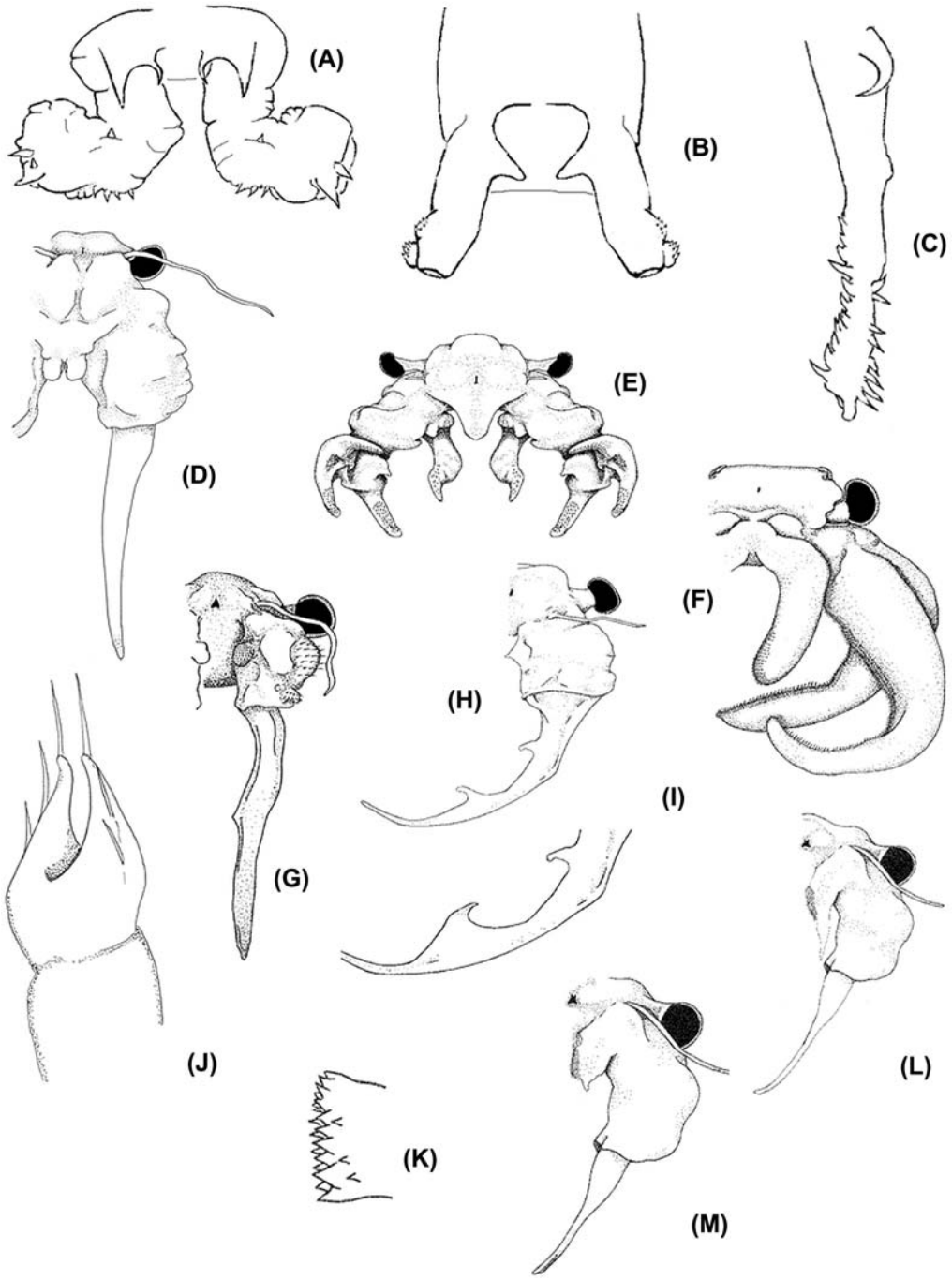


FIGURE 16.2.2 (A) *Tanymastix stagnalis* gonopods, ventral view; (B) *Branchinecta* sp. gonopods, ventral view; (C) *Branchipus schaefferi* right gonopod, ventral view; (D) *Phallocryptus spinosa*, male head, left half, anterior view; (E) *Polyartemiella hazeni* male head anterior view; (F) *Polyartemia forcipata*, male head, left half, anterior view; (G) *Parartemiopsis longicornis*, male head, left half, anterior view; (H) *Artemiopsis bungei*, male head, left half, anterior view; (I) *Artemiopsis plovmornini*, male left second antenna distal antennomere, anterior view; (J) *Branchinectella media*, telson and cercopods; (K) *Linderiella africana*, male left antennal appendage, anterior view; (L) *Linderiella jebalae*, male head, left half, anterior view; (M) *Linderiella massaliensis*, male head, left half, anterior view. *(A and C) After Brendonk & Belk, 1995.*

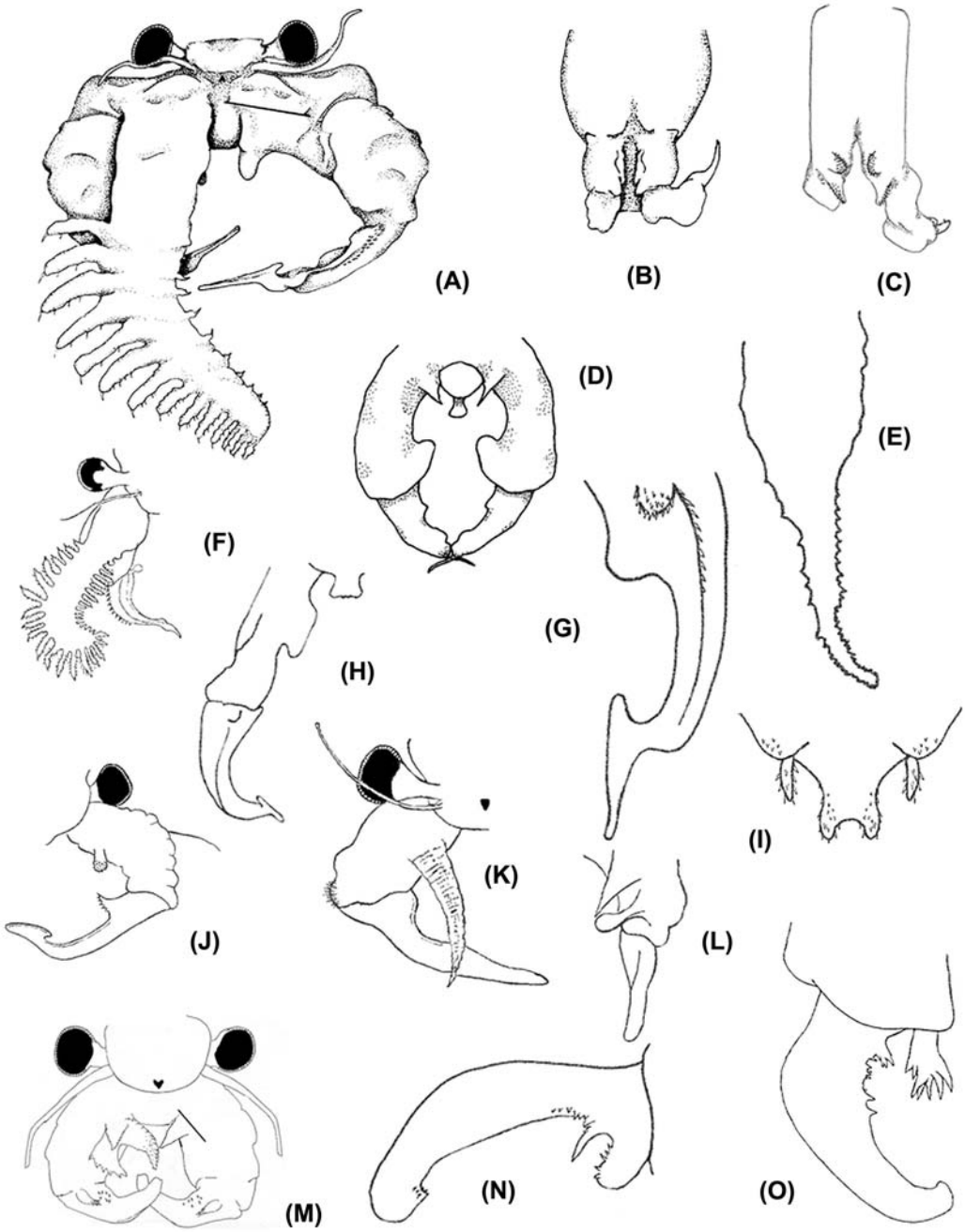


FIGURE 16.2.3 (A) *Eubranchipus uchidai*, male head, anterior view, left antennal appendage removed; (B) *Eubranchipus* sp. gonopods, ventral view, left gonopod everted; (C) *Chirocephalus* sp. gonopods, ventral view, left gonopod everted; (D) *Eubranchipus grubii*, male second antennae and labrum, posterior view; (E) *Eubranchipus vladimiri*, male left antennal appendage, anterior view; (F) *Eubranchipus grubei*, male head, right half, anterior view; (G) *Eubranchipus claviger*, male left second antenna distal antennomere, anterior view; (H) *Eubranchipus rostratus*, male right second antenna, anterior view; (I) *Eubranchipus birostratus*, labral projection; (J) *Chirocephalus bairdi*, male head, left half (antennal appendage omitted) posterior view; (K) *Chirocephalus priscus*, male head, right half, anterior view; (L) *Chirocephalus turkestanicus*, male second antennae, posteriomedial view; (M) *Chirocephalus tereki*, male, head, anterior view, left antennal appendage removed, revealing triangular apophysis; (N) *Chirocephalus slovacicus*, male second antenna distal antennomere, anterior view; (O) *Chirocephalus povlonyi*, male second antenna distal antennomere, anterior view. *(F, H, J, and K) After Daday, 1910; (M) after Brtek, 1984; (O) after Brtek, 1967.*

3′ Second antenna distal antennomere without a small anteriobasal projection, although spines may be present in a line (Fig. 16.2.3 A); apophyses subcylindrical with apex rounded ..... *Eubranchipus* (*Drepanosurus*) *uchidai* (Kikuchi, 1957) [Japan]

4(3) Apophyses present (Fig. 16.2.3 H) 5

4′ Apophyses absent (Fig. 16.2.3 F) ..... *Eubranchipus* (*Siphonophanes*) *grubii* (Dybowski, 1860) [Austria, Czech Republic, Denmark, France, Germany, Hungary, Lithuania, Russia, Poland, Romania, Slovakia, Ukraine]

5(4) Apophyses ridge-like or acute (Fig. 16.2.3 A); labral projection with anteriolateral corners not elongated distally (may be elongated laterally) (Figs. 16.2.3 D, H) 6

5′ Apophyses subcylindrical, rounded apically, and bearing spinulae; labral projection with anteriolateral corners elongated distally (Fig. 16.23 I) ..... *Eubranchipus* (*Drepanosurus*) *birostratus* (Fischer, 1851) [Steppe and wood steppe zones of Eurasia]

6(5) Antennal appendage tapering, shorter than second antennae, lacking large marginal papillae, but bearing small ventral papillae .... *Eubranchipus* (*Drepanosurus*) *hankoi* (Dudich, 1927) [Czech Republic, Hungary, Slovakia]

6′ Antennal appendage lamellar, lateral and distal margins with long papillae ..... *Eubranchipus* (*Drepanosurus*) *rostratus* (Daday, 1910) [Russia]

Branchiopoda: Anostraca: Chirocephalidae: *Chirocephalus*: Species

Note: *Chirocephalus* needs to be revised. *Chirocephalus festae* Colosi, 1922 is known only from the type locality in Cyrenaika, Libya, and is probably not a valid taxon.

1 Apophyses present (Fig. 16.2.3 J) 2

1′ Apophyses absent (Fig. 16.2.3 K) ..... *Chirocephalus priscus* (Daday, 1910) [India, Pakistan]

2(1) Second antennal proximal antennomere with two apophyses each (Fig. 16.2.3 L) 3

2′ Second antennal proximal antennomere with one apophysis each (Fig. 16.2.3 J) 4

3(2) Second antennal distal antennomere arcuate, bending at least 70 degrees medially ..... *Chirocephalus bobrinskii* (Alcock, 1898) [Afghanistan, Kazakhstan, Kyrgyzstan]

3′ Second antennal distal antennomere sinuate, not arcuate (Fig. 16.2.3 M) ..... *Chirocephalus turkestanicus* Daday, 1910 [Kyrgyzstan]

4(2) Apophyses acute (Fig. 16.2.3 M) 5

4′ Apophyses rounded apically (Fig. 16.2.3 J) 12

5(4) Antennal appendage shorter than AII proximal antennomere (Fig. 16.2 3 M) 6

5′ Antennal appendage longer than AII proximal antennomere (Fig. 16.2.4 A) 7

6(5) Second antennal distal antennomere with a distomedial spiniform or triangular process (Fig. 16.2.3 N) .... *Chirocephalus slovacicus* Brtek, 1971 [Slovakia]

6′ Second antennal distal antennomere without a distomedial process (Fig. 16.2.3 M) ..... *Chirocephalus tereki* Brtek, 1984 [Tajikistan]

7(5) Second antennal distal antennomere with a spinose proximal projection (Figs. 16.2.3 O and 16.2.4 A, B) (note: this group needs revision; many of these taxa may be synonyms) 8

7′ Second antennal distal antennomere without a proximal projection ..... *Chirocephalus horribilis* Smirnov, 1948 [Russia]

8(7) Antennal appendage longer lamella with lateral papillae to apex (Figs. 16.2.4 A, B) 9

8′ Antennal appendage longer lamella with lateral papillae on medial margin not present to apex ... *Chirocephalus croaticus* Steuer, 1899 [Croatia]

9(8) Second antenna distal antennomere proximomedial surface with spines, anteriad of medial projection (Fig. 16.2.4 A) 10

9′ Second antenna distal antennomere proximomedial surface without spines, anteriad of medial projection (Fig. 16.2.4 B) .... *Chirocephalus spinicaudatus* Simon, 1886 [France]

10(9) Second antenna distal antennomere proximomedial projection with 6–10 spines 11

10′ Second antenna distal antennomere proximomedial projection with 12 or more spines (Fig. 16.2.4 A) .... *Chirocephalus chyzeri* (Daday, 1890) [Romania, Slovakia]

11(10) Second antenna distal antennomere proximomedial surface with spine row anteriad of medial projection, extending roughly one third the length of the antennomere ..... *Chirocephalus povolnyi* Brtek, 1967 [Afghanistan]

11′ Second antenna distal antennomere proximomedial surface with spine row anteriad of medial projection, extending less than one eighth the length of the antennomere ..... *Chirocephalus robustus* Müller, 1966 [Romania]

12(4) Apophyses subglobular (Fig. 16.2.3 J) 13

12′ Apophyses subconical, cylindrical, or broadly expanded (Figs. 16.2.3 L, M and 16.2.4 C, F) 17

13(12) Antennal appendage with one lamella 14

13′ Antennal appendage with two lamellae, second lamella beneath first 16

14(13) Antennal appendage shorter than AII (Fig. 16.2.4 C) 15

14′ Antennal appendage longer than AII (Fig. 16.2.4 D) ..... *Chirocephalus recticornis* (Brauer, 1877) [Tunisia]

15(14) Second antenna distal antennomere with a prominent posteriolateral projection; antennal appendage short, lobiform ..... *Chirocephalus jaxartensis* (Smirnov, 1948) [Kazakhstan]

15′ Second antenna distal antennomere without a posteriolateral projection; antennal appendage tentacular, medial margin with papillae (Fig. 16.2.4 C) ..... *Chirocephalus shadini* (Smirnov, 1928) [Central Europe to the Urals]

16(13) Antennal appendage with lateral but not medial papillae ..... *Chirocephalus baikalensis* (Naganawa & Orgiljanova, 2000) [Russia]

16′ Antennal appendage with lateral and medial papillae, medial papillae very small ..... *Chirocephalus mongolianus* Uéno, 1940 [China, Mongolia]

17(12) Antennal appendage with one lamella 18

17′ Antennal appendage with two lamellae, second lamella beneath first 21

18(17) AII with distal antennomere bearing a medial low projection (Fig. 16.2.4 E) 19

18′ AII with distal antennomere lacking a medial low projection (Fig. 16.2.4 F) 20

19(18) AII distal antennomere twice as long as proximal antennomere ..... *Chirocephalus carnuntanus* (Brauer, 1877) [Southeastern Europe (Pannonian lowlands and adjacent Czech Republic)]

19′ AII distal antennomere subequal in length to proximal antennomere (Fig. 16.2.4 E) ..... *Chirocephalus josephinae* (Grube, 1853) [Estonia, Poland, Russia, Ukraine; *Chirocephalus ripophilus* (Lepeschkin, 1921) is probably a junior synonym]

20(18) AII distal antennomere proximomedial branch with spines (Fig. 16.2.4 F) ..... *Chirocephalus soulukliensis* Rogers & Soufi, 2013 [Iran]

20′ AII distal antennomere proximomedial branch inerm ..... *Chirocephalus graziellae* (Alonso & Naganawa, 2008) [Mongolia]

21(17) Second antennae distal antennomere with a basal projection (Figs. 16.2.4 A, B, F) 22

21′ Second antennae distal antennomere without a basal projection (Figs. 16.2.4 C, E) 43

22(21) Second antennae distal antennomere with a medial or posteriolateral basal projection (Fig. 16.2.4 H) 23

22′ Second antennae distal antennomere with lateral basal projection (Fig. 16.2.4 G) ..... *Chirocephalus gobisteppensis* (Naganawa & Zagas, 2003) [Mongolia]

23(22) Second antenna distal antennomere excised medially (Figs 16.2.4 H, I) 24

23′ Second antenna distal antennomere not excised medially (Fig. 16.2.4 K) 32

24(23) Antennal appendage longer than second antenna 25

24′ Antennal appendage shorter than second antenna 26

25(24) Second antenna distal antennomere proximomedial branch acute, smooth (Fig. 16.2.4 H) ..... *Chirocephalus nankinensis* (Shen, 1933) [China]

25′ Second antenna distal antennomere proximomedial branch with spines ..... *Chirocephalus sinensis* Thiele, 1907 [China]

26(24) Second antenna distal antennomere arcing medially 70 degrees or more (Fig. 16.2.4 I) 27

26′ Second antennae distal antennomere arcing medially 45 degrees or less (Fig. 16.2.4 J) 28

27(26) Second antenna distal antennomere with an acute or subacute, subapical, medial projection (Fig. 16.2.4 I) ..... *Chirocephalus brteki* Cottarelli, Aygen & Mura, 2010 [Turkey]

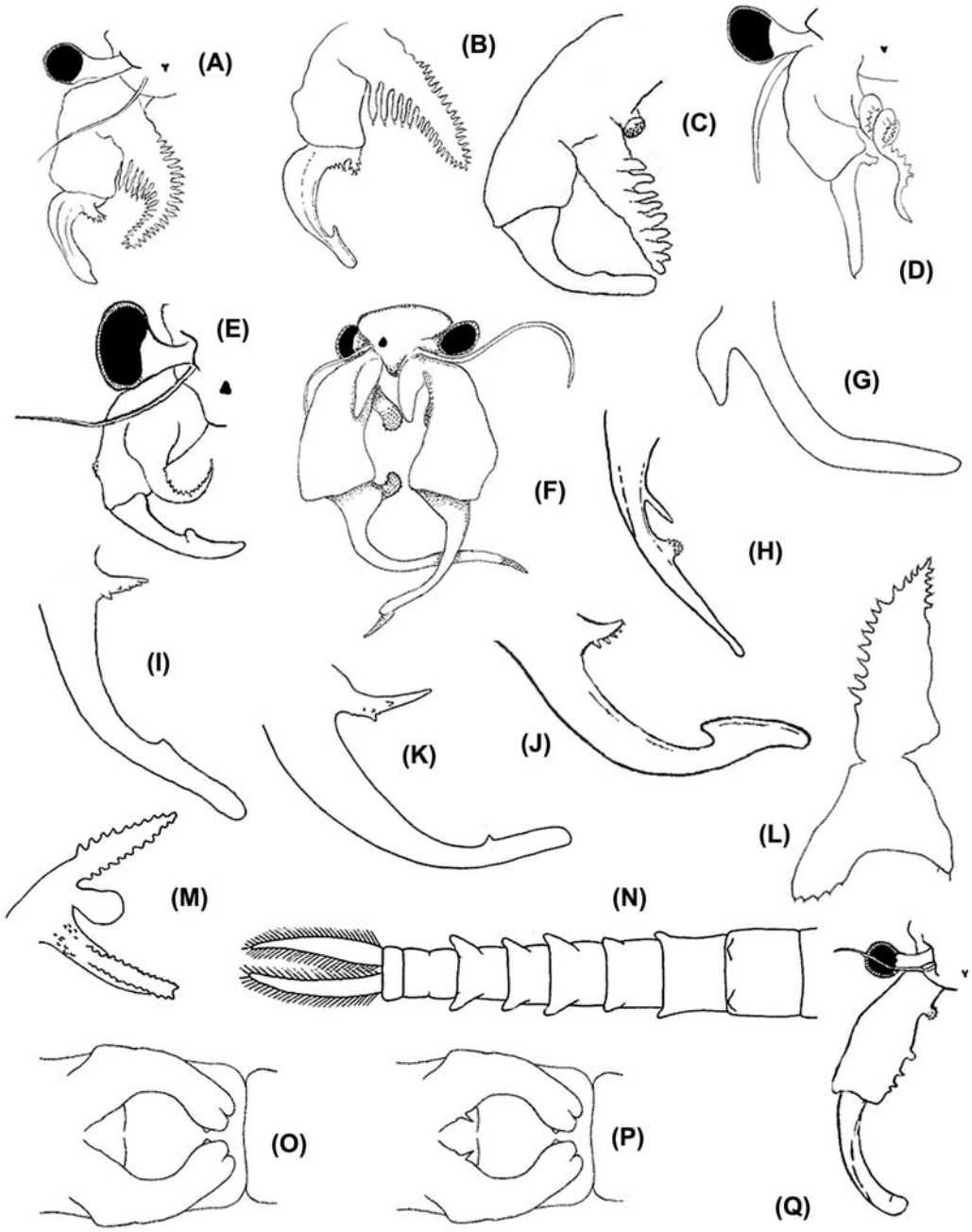


FIGURE 16.2.4 (A) *Chirocephalus chyzeri*, male head, right half, anterior view; (B) *Chirocephalus spinicaudatus*, male right second antenna, anterior view; (C) *Chirocephalus shadini*, male right second antenna, anterior view; (D) *Chirocephalus recticornis*, male head, right half, anterior view; (E) *Chirocephalus josephinae*, male head, right half, anterior view; (F) *Chirocephalus soulukliensis*, male head, anterior view, left oblique; (G) *Chirocephalus gobisteppensis*, male second antenna distal antennomere, anterior view; (H) *Chirocephalus nankinensis*, male second antenna distal antennomere, anterior view; (I) *Chirocephalus brteki*, male second antenna distal antennomere, anterior view; (J) *Chirocephalus bairdi*, male second antenna distal antennomere, anterior view; (K) *Chirocephalus vornatscheri*, male second antenna distal antennomere, anterior view; (L) *Chirocephalus bairdi*, right antennal appendage, upper lamella raised to show lower lamella; (M) *Chirocephalus anatolicus*, right antennal appendage, upper lamella raised to show lower lamella; (N) *Chirocephalus neumanni*, female abdomen dorsal view; (O) *Artemia salina*, gonopods, ventral view; (P) *Artemia franciscana*, gonopods, ventral view; (Q) *Branchinecta tolli*, male head, right half, anterior view. *(A, B, D, E, and Q) After Daday, 1910).*

27′ Second antennae distal antennomere lacking a subapical projection ..... *Chirocephalus kerkyrensis* Pesta, 1936 [Greece, Italy]

28(26) Second antenna distal antennomere proximomedial branch medially directed (Fig. 16.2.4 J) 29

28′ Second antenna distal antennomere proximomedial branch ventrally directed ..... *Chirocephalus orghidani* Brtek, 1966 [Romania]

29(28) Antennal appendage lower lamella entire (Fig. 16.2.4 L) 30

29′ Antennal appendage lower lamella divided (Fig. 16.2.4 M) 31

30(27) Second antenna distal antennomere longer than proximal antennomere ..... *Chirocephalus bairdi* (Brauer, 1877) [Israel, Turkey]

30′ Second antenna distal antennomere subequal to or shorter than proximal antennomere ..... *Chirocephalus brevipalpis* (Orghidan, 1953) [Romania, Serbia]

31(29) Second antenna distal antennomere proximomedial branch smooth, acute ..... *Chirocephalus anatolicus* Cottarelli, Mura, & Özkütük, 2007 [Turkey]

31′ Second antenna distal antennomere proximomedial branch spinose ..... *Chirocephalus murae* Brtek & Cottarelli, 2006 [Turkey]

32(23) Second antenna distal antennomere lacking a subapical projection 33

32′ Second antenna distal antennomere with a short subapical projection (Fig. 16.2.4 K) ..... *Chirocephalus vornatscheri* Brtek, 1968 [Bulgaria, Turkey]

33(32) Second antenna distal antennomere longer than proximal antennomere 34

33′ Second antenna distal antennomere subequal to or shorter than proximal antennomere 39

34(33) Female abdomen with lateral projections (Fig. 16.2.4 N) 35

34′ Female abdomen smooth 38

35(34) Female abdominal lateral projections rounded 36

35′ Female abdominal lateral projections acute; male second antennal distal antennomere basomedial projection recurved apically ..... *Chirocephalus paphlogonicus* Cottarelli, 1971 [Turkey. *Chirocephalus ludmilae* Vekhoff, 1992 is probably a junior synonym]

36(35) Female without dorsal projection on genital segments 37

36′ Female with dorsal projection on genital segments ..... *Chirocephalus diaphanus* Prévost, 1803 [western Palaearctic]

37(36) Female with brood pouch smooth ..... *Chirocephalus tauricus* Pesta, 1921 [Turkey]

37′ Brood pouch with lateral projections ..... *Chirocephalus neumanni* Hartland-Rowe, 1967 [Iran, Israel]

38(34) Antennal appendage upper lamella apex triangular, with subtending marginal papillae ..... *Chirocephalus algidus* Cottarelli, Aygen & Mura, 2010 [Turkey]

38′ Antennal appendage upper lamella apex digitiform, elongated, without marginal papillae ..... *Chirocephalus weisigi* Smirnov, 1933 [Azerbaijan]

39(33) Second antenna distal antennomere with a strong proximal bend medially, distally straight 40

39′ Second antenna distal antennomere straight or sinuate ..... *Chirocephalus sibyllae* Cottarelli & Mura, 1975 [Italy]

40(39) Second antenna distal antennomere subequal in length to proximal 41

40′ Second antenna distal antennomere shorter than proximal 42

41(40) Second antenna distal antennomere with proximomedial projection less than one fourth the length of the antennomere, smooth ..... *Chirocephalus cupreus* Cottarelli, Mura, & Özkütük, 2007 [Turkey]

41′ Second antenna distal antennomere with proximomedial projection at least one third the length of the antennomere, with many small denticles ..... *Chirocephalus pelagonicus* Petkovski, 1986 [Macedonia]

42(40) Antennal appendage lower lamella broadly rounded medially ..... *Chirocephalus appendicularis* Vavra, 1905 [Lebanon, Syria, Turkey]

42′ Antennal appendage lower lamella broadly triangular ..... *Chirocephalus salinus* Daday, 1910/*Chirocephalus reiseri* Marcus, 1913 [Bosnia & Herzegovina, France, Italy]

43(21) Antennal appendage subequal to or longer than second antennae 44

43′ Antennal appendage shorter than second antennae ..... *Chirocephalus ruffoi* Cottarelli & Mura, 1984 [Italy]

44(43) Antennal appendage subequal in length to second antennae; second antennal distal antennomere more or less straight, lacking a medial projection 45

44′ Antennal appendage more than twice as long as second antennae; second antennal distal antennomere curved medially, with a small medial projection ..... *Chirocephalus wangi* Hsu, 1933 [China]

45(44) Second antennal distal antennomere with apex directed distally 46

45′ Second antennal distal antennomere with apex directed laterally; antennal appendage with marginal papillae longer on medial margin ..... *Chirocephalus marchesonii* Ruffo & Vesentini, 1957 [Italy]

46(45) Antennal appendage with marginal papillae subequal in size, roughly as long as broad ..... *Chirocephalus ponticus* Beladjal & Mertens, 1997 [Turkey]

46′ Antennal appendage with marginal papillae 3–10 times longer than wide ..... *Chirocephalus skorikowi* Daday, 1913 [Russia]

Branchiopoda: Anostraca: Artemiidae: *Artemia*: Species

Artemia contains the brine shrimps, all halophiles, sometimes known as "sea monkeys." Most morphological characters are plastic, and wild collected animals may vary greatly, depending upon environmental conditions. Furthermore, there are several independent parthenogenic strains that have arisen from different species and are not generally separable without genetic analyses. Molecular analysis is the only really reliable tool for separating *Artemia* species. Two species are invasive in the Palaearctic.

1 Gonopods without basolateral spiniform projections (Fig. 16.2.4 O) 2

1′ Gonopods with basolateral spiniform projections (Fig. 16.2.4 P) 3

2(1) Egg diameter less than 250 µm; male second antennae with apophyses subconical ..... *Artemia salina* (Linneaus, 1758) [Western and central Palaearctic. Afrotropical]

2′ Egg diameter greater than 300 µm; male second antennae with apophyses subspherical ..... *Artemia tibetiana* Abatzopoulos, Zhang & Sorgeloos, 1998 [China]

3(1) Brood pouch with a ventral pair of large spines; male apophyses with microspinulae (need compound microscope) generally in pairs or triplets 4

3′ Brood pouch without a ventral pair of large spines; male apophyses with microspinulae (need compound microscope) single, well separated ..... *Artemia persimilis* Piccinelli & Prosdocimi, 1968 [Invasive in Italy, but may no longer be extant. Neotropical]

4(3) Cercopods each with five or less setae situated apically ..... *Artemia urmiana* Gunther, 1899 [Iran]

4′ Cercopods each with 10 or more setae generally distributed along distal margins ..... *Artemia franciscana* Kellogg, 1906 [Invasive Mediterranean region. Nearctic, Neotropical]

OR ..... *Artemia sinica* Cai, 1989 [China]

Branchiopoda: Anostraca: Branchinectidae: *Branchinecta*: Species

1 Male second antennae inerm (Fig. 16.2.1 N), at most bearing dense, tiny spinulae 2

1′ Male second antennae proximal antennomere, with medial surface bearing spines (Figs. 16.2.4 Q and 16.2.5 E) 4

2(1) Gonopod with proximal lobe not overreaching the ventrolateral spine (Fig. 16.2.5 A) 3

2′ Gonopod with proximal lobe overreaching the ventrolateral spine (Fig. 16.2.5 B); labrum apex conical, covered with fine setulae (Fig. 16.2.1 P) ..... *Branchinecta orientalis* Sars, 1901 [Widespread]

3(2) Cercopods with plumose setae on medial margins only (Fig. 16.2.5 C); labrum apex inerm (Fig. 16.2.1 O) ..... *Branchinecta ferox* (Milne-Edwards, 1840) [Central and western Palaearctic]

3′ Cercopods with plumose setae on medial and lateral margins (Fig. 16.2.5 D) ..... *Branchinecta minuta* Smirnov, 1948 [Russia]

4(1) Male second antennae proximal antennomere with medial surface bearing a longitudinal row of spines; pulvillus not projecting, flat (Fig. 16.2.5 E) 5

4′ Male second antennae proximal antennomere with medial surface bearing spines at distal end; pulvillus projecting, rounded (Fig. 16.2.4 Q) ..... *Branchinecta tolli* (Sars, 1897) [Russia]

5(4) Male second antennae proximal antennomere, with medial longitudinal spine row extending at least two thirds the length of the antennomere (Fig. 16.2.5 E) ..... *Branchinecta paludosa paludosa* (Müller, 1788) [Circumpolar]

5′ Male second antennae proximal antennomere, with medial longitudinal spine row extending only one half the length of the antennomere (Fig. 16.2.5 F) ..... *Branchinecta paludosa tjanshanica* Akatova, 1987 [Kyrgyzstan]

Branchiopoda: Anostraca: Streptocephalidae: *Streptocephalus*: Species

Modified from Hamer et al. (1994).

1 Eggs spherical; male antennal appendage with or without a spur, if spur present, then a lobiform or triangular projection is present distobasally to the spur OR if the projection is absent, then the "finger" apex is directed anteriorly (Figs. 16.2.5 H, I); subgenus *Streptocephalus* 2

1′ Eggs tetrahedral; male antennal appendage without a projection distobasally to the spur and the "finger" apex is directed distally, only curving slightly; subgenus *Parastreptocephalus* (Fig. 16.2.5 G) ..... *Streptocephalus* (*Parastreptocephalus*) *sudanicus* Daday, 1910 [Chad, Mali, Niger, Senegal, Sudan]

2(1) Male antennal appendage with a spur (Fig. 16.2.5 I) 3

2′ Male antennal appendage without a spur (Fig. 16.2.5 H) ..... *Streptocephalus rothschildi* Daday, 1908 [Northeast Africa]

3(2) Antennal appendage "thumb" with spur subtended by a lobiform or triangular projection distobasally 4

3′ Antennal appendage "thumb" with spur lacking any subtending projection distobasally ..... *Streptocephalus bimaris* Gurney, 1909 [Tunisia]

4(3) Spur shorter than or equal to the basal width or the "thumb" (Fig. 16.2.5 I) 5

4′ Spur longer than the basal width of the "thumb" (Fig. 16.2.5 G) 6

5(4) Male frontal appendage divided into two long medial rami and two shorter lateral rami (Fig. 16.2.5 K) ..... *Streptocephalus bouvieri* Daday, 1908 [Chad, Uganda]

5′ Male frontal appendage divided into two rami (Fig. 16.2.5 J) ..... *Streptocephalus zeltneri* Daday, 1910 [Senegal, Sudan]

6(4) Frontal appendage long, with branches or numerous spines (Figs. 16.2.5 L, M) 7

6′ Frontal appendage simple, may be bifurcated (Fig. 16.2.5 N) 8

7(6) Frontal appendage with three primary rami (Fig. 16.2.5 N) ..... *Streptocephalus neumanni* Thiele, 1904 [Ethiopia, Yemen]

7′ Frontal appendage may be bifurcate apically, ventral surface with numerous spines (Fig. 16.2.5 M) ..... *Streptocephalus probiscideus* (Frauenfeld, 1873) [Sudan]

8(7) Antennal appendage "thumb" with spur subtended by a single lobiform or triangular projection distobasally (Figs. 16.2.5 O, P) 9

8′ Antennal appendage "thumb" with spur subtended by a lobiform or triangular project ion distobasally ..... *Streptocephalus vitreus* (Brauer, 1877) [Chad, Sudan. Afrotropical]

9(8) Antennal appendage "finger" a single ramus (Fig. 16.2.5 O) 10

9′ Antennal appendage "finger" with two rami, primary ramus margined with spines (Fig. 16.2.5 P) ..... *Streptocephalus simplex* Gurney, 1906 [Arabian Peninsula, India, Pakistan]

10(9) Antennal appendage with "finger" roughly one third the length of the "thumb"; "thumb" with spines all along anterior margin (Fig. 16.2.5 O) ..... *Streptocephalus rubricaudatus* (Klunzinger, 1867) [Northern Africa]

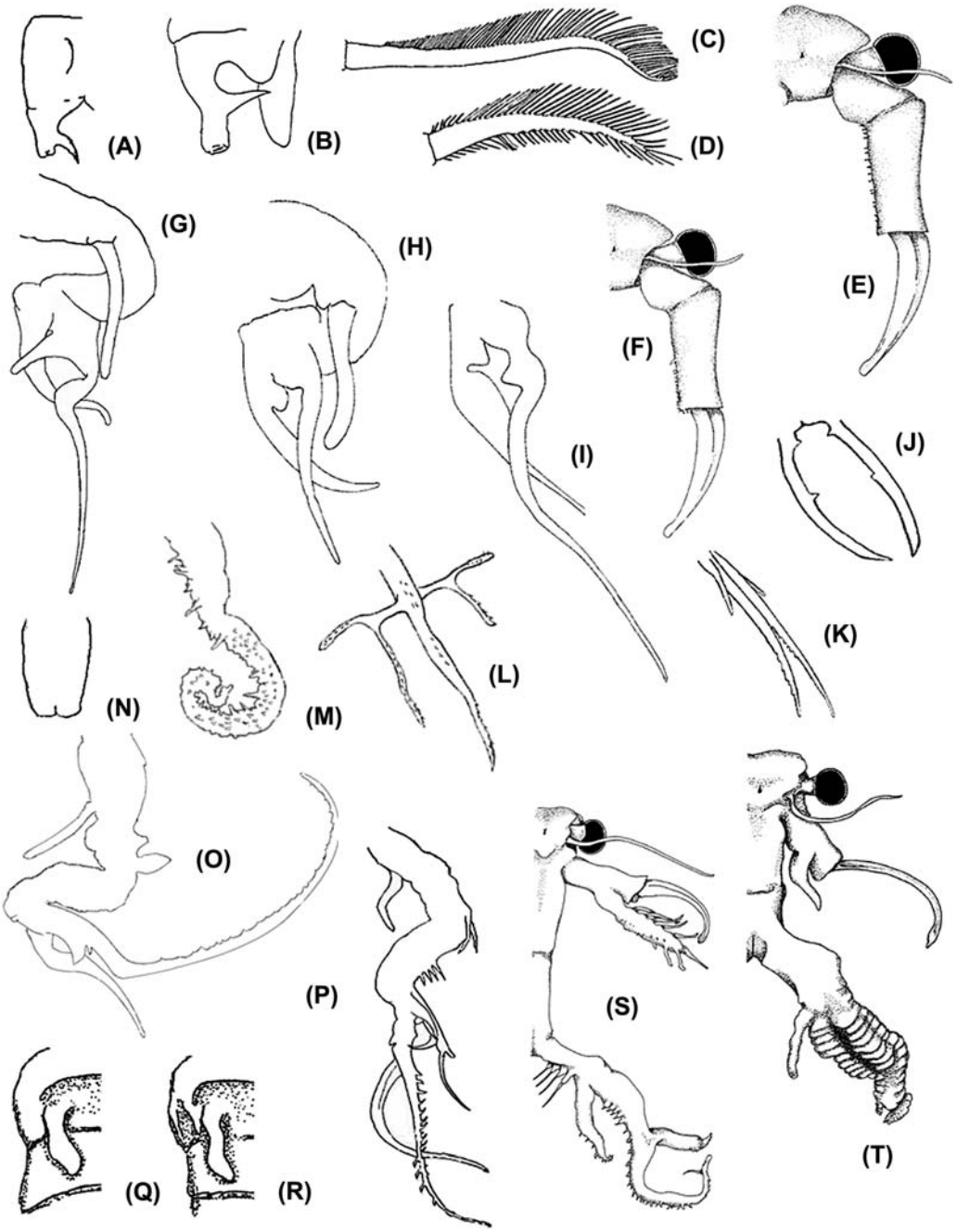


FIGURE 16.2.5 (A) *Branchinecta minuta*, right gonopod, retracted, ventral view; (B) *Branchinecta orientalis*, right gonopod, retracted, ventral view; (C) *Branchinecta ferox*, right cercopod, dorsal view; (D) *Branchinecta minuta*, right cercopod, dorsal view; (E) *Branchinecta paludosa*, male head, left half, anterior view; (F) *Branchinecta paludosa tjanshanica*, male head, left half, anterior view; (G) *Streptocephalus sudanicus*, male, right second antenna, lateral view; (H) *Streptocephalus rothschildi*, male, right second antenna, lateral view; (I) *Streptocephalus zeltneri*, male, right antennal appendage, lateral view; (J) *Streptocephalus zeltneri*, male, frontal appendage, anteriolateral oblique view; (K) *Streptocephalus bouvieri*, male, frontal appendage, anteriolateral oblique view; (L) *Streptocephalus neumanni*, male, frontal appendage, anteriolateral oblique view; (M) *Streptocephalus probiscideus*, male, frontal appendage, anteriolateral oblique view; (N) *Streptocephalus rubricaudatus*, male, frontal appendage, dorsal view; (O) *Streptocephalus rubricaudatus*, male, right second antenna, lateral view; (P) *Streptocephalus simplex*, male, right second antenna, lateral view; (Q) *Branchinella kugenumaensis*, gonopods, ventral view; (R) *Branchinella chudeaui*, gonopods, ventral view; (S) *Branchinella kugenumaensis*, male head, left half, anterior view; (T) *Branchinella hardingi*, male head, left half, anterior view.

10′ Antennal appendage with "finger" and "thumb" subequal in length; "thumb" with few spines in a proximal group on anterior margin .... *Streptocephalus torvicornis* (Waga, 1842)
[Mediterranean region, eastern Europe, Ponto Caspian region]

Branchiopoda: Anostraca: Thamnocephalidae: Genera

1 Male abdominal segments with long ventral spines; frontal appendage shorter than second antennae, bilobed (Fig. 16.2.2 D) .... ***Phallocryptus***
[Halophile; Palaearctic east to Mongolia, in Africa south to Botswana]

1′ Male abdominal segments lacking spines; frontal appendage longer than second antennae, biramal ..... ***Branchinella***

Branchiopoda: Anostraca: Thamnocephalidae: *Phallocryptus*: Species

1 Frontal appendage inerm; male abdominal segment XII with a ventrolateral conical protrusion just lateral of the gonopod base that has its length less than half the gonopod basal width; male rostrum in lateral view with angularly apex bent 90°; frontal appendage shorter than second antennae, bilobed (Fig. 16.2.2 D) ..... *Phallocryptus spinosa* (Milne-Edwards, 1840)
[Widespread. Afrotropical]

1′ Frontal appendage apically with a few small spines; male abdominal segment XII with a large ventrolateral chitinized conical spiniform process just lateral of the gonopod base, that has its length at least half the basal width of the gonopod or longer; male rostrum in lateral view with apex arcing 90° ..... *Phallocryptus tserensodnomi* Alonso & Ventura, 2013
[Mongolia]

Branchiopoda: Anostraca: Thamnocephalidae: *Branchinella*: Species

1 Male second antenna antennal appendage with marginal spines (Fig. 16.2.5 S) 2

1′ Male second antenna antennal appendage without marginal spines (Fig. 16.2.5 T) .... *Branchinella* (*Branchinellites*) *hardingi* (Qadri & Baqai, 1956)
[India, Pakistan]

2(1) Male gonopod with a large, basolateral subconical or subcylindrical lobe (Fig. 16.2.5 R) .... *Branchinella* (*Branchinellites*) *chudeaui* (Daday, 1910)
[Chad, Gambia, Niger, Senegal]

2′ Male gonopod lacking a basolateral lobe (Fig. 16.2.5 Q) ..... *Branchinella* (*Branchinellites*) *kugenumaensis* (Ishikawa, 1895)
[China, Japan, South Korea, Taiwan]

Branchiopoda: Anostraca: Tanymastigidae: Genera

1 Gonopods each with a ventral lamellar projection, with distomedial edge not margined with spines, but may have a single medial spine (Fig. 16.2.2 A) ..... ***Tanymastix*** **[p. 658]**

1′ Gonopods each with a ventral lamellar projection, with distomedial edge margined with spines ..... ***Tanymastigites*** **[p. 660]**

Branchiopoda: Anostraca: *Tanymastix*: Species

1 Frontal appendage with first basolateral sub-branch longer than second sub-branch (Fig. 16.2.6 F) 2

1′ Frontal appendage with first basolateral sub-branch shorter than or equal in length to second sub-branch (Fig. 16.2.6 E) 3

2(1) Second antennal proximal antennomere with ventrodistal projection falcate (Fig. 16.2.6 D) ..... *Tanymastix affinis* Daday, 1910
[Morocco]

2′ Second antennal proximal antennomere with ventrodistal projection broadly rounded with a digitiform lateral projection (Fig. 16.2.6 B) ..... *Tanymastix stagnalis* (Linneaus, 1758)
[Europe, North Africa]

3(1) Second antennal proximal antennomere with ventrodistal projection bearing angular, projecting lateral corners (Fig. 16.2.6 C) .... *Tanymastix motasi* Orghidan, 1945
[Macedonia, Romania]

3′ Second antennal proximal antennomere with ventrodistal projection smooth (Fig. 16.2.6 A) ..... *Tanymastix stellae* Cottarelli, 1967
[France, Italy]

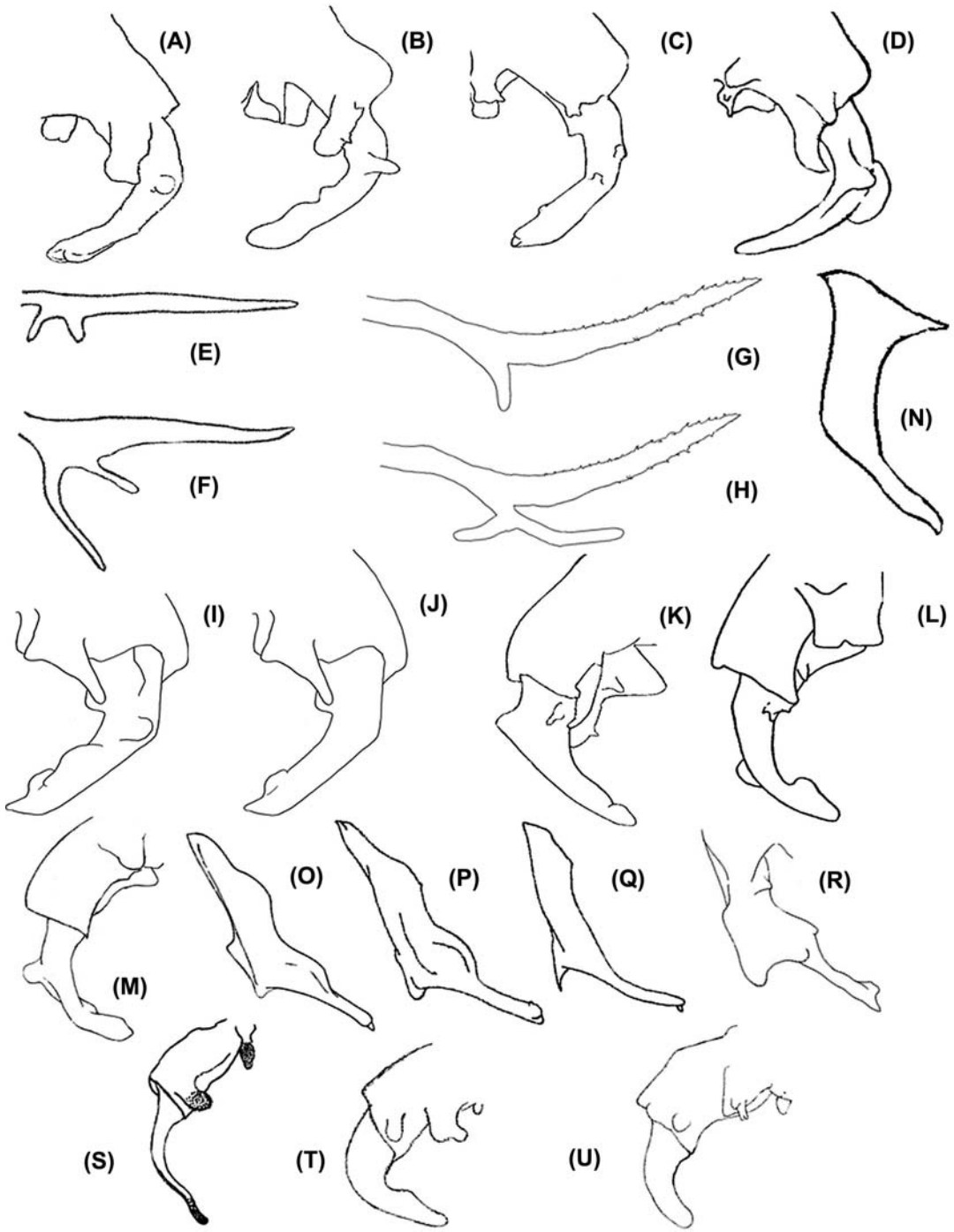


FIGURE 16.2.6 (A) *Tanymastix stellae*, male, right second antenna, posterior view; (B) *Tanymastix stagnalis*, male, right second antenna, posterior view; (C) *Tanymastix motasi*, male, right second antenna, posterior view; (D) *Tanymastix affinis*, male, right second antenna, posterior view; (E) *Tanymastix motasi*, antennal appendage; (F) *Tanymastix affinis*, antennal appendage; (G) *Tanymastigites lusitanica*, antennal appendage; (H) *Tanymastigites mzabica*, antennal appendage; (I) *Tanymastigites lusitanica*, male, right second antenna, posterior view, antennal appendage absent; (K) *Tanymastigites mzabica*, left second antenna, anterior view, antennal appendage absent; (L) *Tanymastigites cyrenaica*, left second antenna, anterior view, antennal appendage absent; (M) *Tanymastigites brteki*, left second antenna, anterior view, antennal appendage absent; (N) *Branchipus laevicornis*, male right second antenna, distal antennomere, anterior view, antennal appendages absent; (O) *Branchipus blanchardi*, male right second antenna, distal antennomere, anterior view, antennal appendages absent; (P) *Branchipus intermedius*, male right second antenna, distal antennomere, anterior view, antennal appendages absent; (Q) *Branchipus schaefferi*, male right second antenna, distal antennomere, anterior view, antennal appendages absent; (R) *Branchipus cortesi*, male right second antenna, distal antennomere, anterior view, antennal appendages absent; (S) *Branchipodopsis abidai*, male right second antenna, distal antennomere, anterior view; (T) *Branchipodopsis affinis*, male right second antenna, distal antennomere, anterior view; (U) *Branchipodopdsis relictus*, male right second antenna, distal antennomere, anterior view.

Branchiopoda: Anostraca: Tanymastigites: Species

Modified from Machado & Sala (2013).

1	Antennal appendage main branch, lateral ramus undivided (Fig. 16.2.6 G) 2
1′	Antennal appendage main branch, lateral ramus divided (Fig. 16.2.6 H) 3
2(1)	Second antenna distal antennomere with a ventrolateral ridge approximately at maximum point of curvature (Fig. 16.2.6 I) ..... *Tanymastigites lusitanica* Machado & Sala, 2013 [Portugal]
2′	Second antenna distal antennomere without such a ventrolateral ridge (Fig. 16.2.6 J) ..... *Tanymastigites perrieri* (Daday, 1910) [Northeast Africa]
3(1)	Second antenna medially fused proximal antennomeres with anterior and distal projections (Figs. 16.2.6 L, M) 4
3′	Second antenna medially fused proximal antennomeres without anterior and distal projections (Fig. 16.2.6 K) ..... *Tanymastigites mzabica* (Gauthier, 1928) [Algeria]
4(3)	Second antenna medially fused proximal antennomeres with anterior projections low, inconspicuous, length < basal width; distal lamellar projections quadrate, with distal margin emarginate (Fig. 16.2.6 L) ..... *Tanymastigites cyrenaica* Brtek, 1972 [Libya, Saudi Arabia]
4′	Second antenna medially fused proximal antennomeres with anterior projections prominent, conical, apically rounded, length ≥ basal width; distal lamellar projections with distal margins sinuate (Fig. 16.2.6 M) ..... *Tanymastigites brteki* Thiéry, 1986 [Morocco]

Branchiopoda: Anostraca: Branchipodidae: Genera

1	Male with frontal appendages ..... ***Branchipus*** **[p. 660]**
1′	Male without frontal appendages ..... ***Branchipodopsis*** **[p. 660]**

Branchiopoda: Anostraca: *Branchipus*: Species

1	Second antenna, distal antennomere lateral angle projecting (Fig. 16.2.6 O) 2
1′	Second antenna, distal antennomere lateral angle rounded (Fig. 16.2.6 N) ..... *Branchipus laevicornis* Daday, 1912 [Turkey]
2(1)	Second antenna, distal antennomere lateral projection digitiform (Figs. 16.2.6 P, Q) 3
2′	Second antenna, distal antennomere lateral projection flanged (Fig. 16.2.6 O) 4
3(2)	Male abdomen with ventrolateral cornified projections ..... *Branchipus intermedius* Orghidan, 1947 [Romania]
3′	Male abdomen smooth ..... *Branchipus schaefferi* Fischer, 1834 [Northern Africa, temperate Europe, east to Pakistan, north to Russia]
4(2)	Second antenna, distal antennomere lateral projection less than one third the length of the antennomere (Fig. 16.2.6 O) ..... *Branchipus blanchardi* Daday, 1908 [France, Italy]
4′	Second antenna, distal antennomere lateral projection one half to one third the length of the antennomere (Fig. 16.2.6 R) ..... *Branchipus cortesi* Alonso & Jaume, 1991 [Spain]

Branchiopoda: Anostraca: *Branchipodopsis*: Species

1	Male second antennal distal antennomere with apex lacking depressions 2
1′	Male second antennal distal antennomere with apex concave on later surface; proximal antennomere with anterior projection medial lobe apically explanate ..... *Branchipodopsis buettikeri* Thiéry & Jean, 2004 [Oman]
2(1)	Male second antenna, proximal antennomere with a medial and a distal projection (Figs. 16.2.6 T, U) 3
2′	Male second antenna, proximal antennomere with a distal projection only (Fig. 16.2.6 S) ..... *Branchipodopsis abiadi* (Brauer, 1877) [Sudan, western Sahara]

3(2) Male second antenna, proximal antennomere with proximal projection, bearing a medial acute process that is longer that the other apical processes (Fig. 16.2.6 T) ..... *Branchipodopsis affinis* Sars, 1901 [China, Mongolia, Russia. Oriental region]

3′ Male second antenna, proximal antennomere with proximal projection, bearing a medial acute process that is shorter that the other apical processes (Fig. 16.2.6 U) ..... *Branchipodopsis relictus* Van Damme, Dumont, & Weekers, 2004 [Yemen: Socotra]

Branchiopoda: Notostraca: Triopsidae: Genera

One family: Triopsidae Kielhack, 1910.

1 Telson without a caudal lamina projecting between cercopods (Fig. 16.2.7 B) ..... ***Triops*** **[p. 661]**

1′ Telson with a caudal lamina projecting between cercopods (Fig. 16.2.7 A) ..... ***Lepidurus*** **[p. 661]**

Branchiopoda: Notostraca: Triopsidae: *Triops*: Species

Adapted from Longhurst (1955), this genus is in need of revision. *Triops cancriformis* is a complex of at the very least five species. Definitive morphological characters are lacking to separate some taxa (Korn et al., 2006), while others can only be determined based on large series of specimens (Korn et al., 2009). The best method for discriminating species in this group is using molecular techniques (Korn et al., 2009).

1 Second maxilla present (Fig. 16.2.7 C) 2

1′ Second maxilla absent (Fig. 16.2.7 D) ..... *Triops* "*longicaudatus*" (LeConte, 1846) [invasive: China (?), Japan, Korea. Americas (in need of revision)]

2(1) Apodus somites with distal margin bearing acute or rounded spines, ventral somite surface with small, scattered supranumerary spines (Fig. 16.2.7 E) 3

2′ Apodus somites with distal margin bearing acute spines, otherwise ventral somite surface without spines (Fig. 16.2.7 F) .... *Triops cancriformis* (Bosc, 1756) complex, sensu Korn et al. 2006, 2009 [Palaearctic. Afrotropical, Oriental]

3(2) Midthoracic peropods with endopod elongated, apex subacute; pereopod VI exopod margin with small spines interspersed with scattered large spines two times or more the length of the small spines 4

3′ Midthoracic peropods with endopod not elongated, apex rounded; pereopod VI exopod margin with subequal spines .... *Triops granarius* (Lucas, 1864) [Palaearctic. Afrotropical, Oriental]

4(3) Pereopod VI exopod margin with more large spines than small spines; large spines about two times the length of the small spines; female with large spines generally distributed ..... *Triops multifidus* Korn & Hundsdoerfer, 2016 [Morocco]

4′ Pereopod VI exopod margin with more small spines than large; large spines 3−4 times the length of the small spines; female with large spines primarily in proximal half ..... *Triops maximus* Korn & Hundsdoerfer, 2016 [Morocco]

Branchiopoda: Notostraca: *Lepidurus*: Species

Adapted from Longhurst (1955).

1 Less than 30 somites 2

1′ More than 30 somites 4

2(1) Caudal lamina three to four times longer than telson; thoracopod I with endite V greatly surpassing carapace margin 3

2′ Caudal lamina as long as telson, with 0−5 medial spines; thoracopod I with endite V not or just barely surpassing carapace margin .... *Lepidurus arcticus* (Pallas, 1793) [circumboreal]

3(2) Caudal lamina with 20−100 medial spines on a strong central keel ..... *Lepidurus apus* (L. 1758) [Europe]

3′ Caudal lamina with three to 25 medial spines on a weak central keel ..... *Lepidurus lubbocki* (Brauer, 1873) [Mediterranean basin]

4(1) Caudal lamina at least twice as long as broad, length/maximum width ratio ~2.3 ..... *Lepidurus batesoni* Longhurst, 1955 [Kazakhstan]

4′ Caudal lamina broadly explanate and depressed, length/maximum width ratio 0.8 to 1.5 ..... *Lepidurus mongolicus* Vekhov, 1992 [Mongolia]

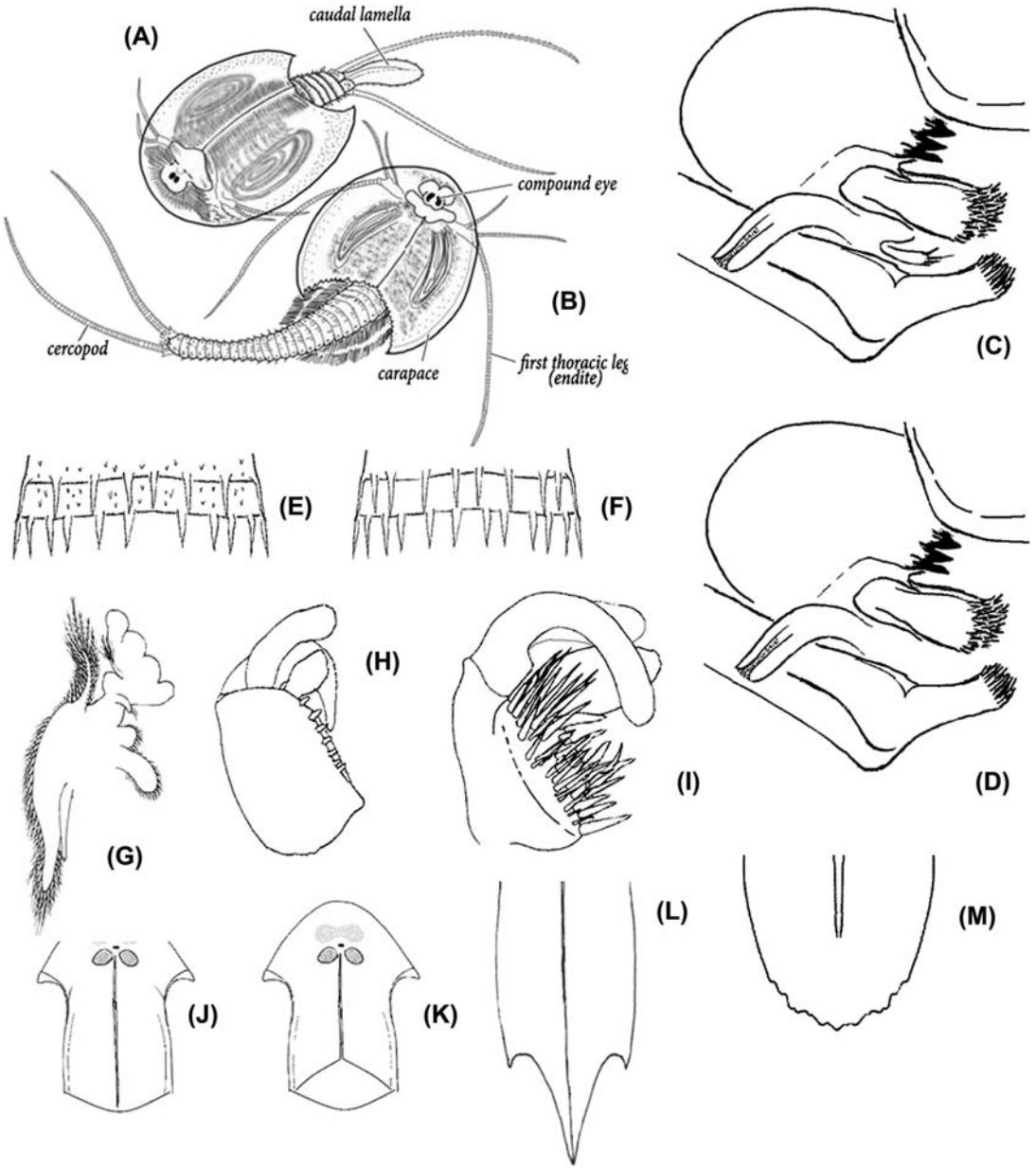


FIGURE 16.2.7 (A) *Lepidurus* sp. general aspect; (B) *Triops* sp. general aspect; (C) *Triops granarius*, mouth parts, right side, ventral view; (D) *Triops* "*longicaudatus*", mouth parts, right side, ventral view; (E) *Triops granarius*, apodous abdominal body rings, ventral view; (F) *Triops cancriformis*, apodous abdominal body rings, ventral view; (G) *Lynceiopsis perrieri*, male thoracopod II, anterior view; (H) *Lynceus simiaefacies*, male right clasper, lateral view (setae not shown); (I) *Lynceus biformis*, male right clasper, lateral view (setae not shown); (J) *Lynceus* sp., head anterior view; (K) *Lynceus* sp., head anterior view; (L) *Lynceus brachyurus*, female rostrum, anterior view; (M) *Lynceus biformis*, female rostrum, anterior view. *(G) Redrawn from Martin & Belk (1989).*

Branchiopoda: *Diplostraca*: Suborders

1	Carapace folded, no true hinge present laterally flattened OR carapace reduced or absent (Figs. 16.2.1 C, F, K–M) 2
1′	Carapace with a true, interlocking dorsal hinge; carapace subglobular, smooth, without growth lines, containing entire animal including head (Figs. 16.2.1 D, E) ..... Laevicaudata, one family: **Lynceidae [p. 663]**
2(1)	Carapace encompassing head, growth lines present, although may be faint (Figs. 16.2.1 C, F) 2
2′	Carapace, if present, not encompassing head, growth lines absent (Figs. 16.2.8–47) ..... **Cladocera [p. 664]**
3(2)	First antenna smooth, without lobes along anterior surface (Fig. 16.2.1 F) ..... Cyclestherida, *Cyclestheria* sp. [Circumtropical and subtropical. Probably many cryptic species]
3′	First antenna with a longitudinal series of lobes on anterior surface (Fig. 16.2.1 C) ..... **Spinicaudata [p. 720]**

Branchiopoda: Laevicaudata: Lynceidae: Genera

One family: Lynceidae Stebbing, 1902.

1	Male thoracopod II with a large distal lobed process (Fig. 16.2.7 G) ..... ***Lynceiopsis* [p. 663]**
1′	Male thoracopod II similar to thoracopod III or, if modified, lacking a large distal lobed process ..... ***Lynceus* [p. 663]**

Branchiopoda: Laevicaudata: *Lynceiopsis*: Species

1	Male thoracopod I clasper with movable finger ventral margin convex in lateral view; lamina abdominalis with posterior lobe larger than anterior and medial lobes, all lobes straight ..... *Lynceiopsis perrieri* Daday, 1912 [Niger]
1′	Male thoracopod I clasper with movable finger ventral margin sinuate in lateral view; lamina abdominalis with lobes subequal, medial lobe arcing anteriorly ..... *Lynceiposis sancti-johanni* Thiéry, 1986 [Chad]

Branchiopoda: Laevicaudata: *Lynceus*: Species

Modified from Rogers et al. (2016).

1	First thoracopod pair modified as claspers (males) 2
1′	First thoracopod pair not modified as claspers (females, note: female *Lynceus mandsuricus* unknown) 5
2(1)	Clasper endopod (so-called “movable finger”) reaching nearly to or slightly beyond endite III (so called “gripping area”) (Fig. 16.2.7 I) 3
2′	Clasper endopod barely reaching middle of endite III (Fig. 16.2.7 H) ..... *Lynceus simiaefacies* Harding, 1941 [Yemen]
3(2)	Rostral keel entire or bifurcate in apical half (Fig. 16.2.7 K) 4
3′	Rostral keel bifurcate just distad of the setal fields ..... *Lynceus mandsuricus* Daday, 1927 [China]
4(3)	Clasper in lateral view with “palm” region planar (Fig. 16.2.7 I) ..... *Lynceus biformis* (Ishikawa, 1895) [China, Japan, Korea, Russia, Taiwan]
4′	Clasper in lateral view with “palm” anterior margin arcuate ..... *Lynceus brachyurus* Müller, 1776 [Holarctic]
5(1)	Rostrum with medial carina entire (Figs. 16.2.7 J, L) 6
5’	Rostrum with medial carina bifurcate distal third (Fig. 16.2.7 K) ..... *Lynceus simiaefacies* Harding, 1941 [Yemen]
6(5)	Rostrum distal margin with lateral angles produced, apex entire (Fig. 16.2.7 L) ..... *Lynceus brachyurus* Müller, 1776 [Holarctic]
6′	Rostrum distal margin denticulate (Fig. 16.2.7 M) ..... *Lynceus biformis* (Ishikawa, 1895) [China, Japan, Korea, Russia, Taiwan]

Branchiopoda: Diplostraca: Cladocera: Suborders

1	Trunk and thoracic limbs entirely or almost entirely covered by carapace; thoracic limbs semifoliaceous 2
1′	Trunk and thoracic limbs not covered by carapace; thoracic limbs stenopodous, clearly segmented 3
2(1)	Six pairs of thoracic limbs, five anterior of which are of similar structure, bearing numerous long filtering setae ... **Ctenopoda [p. 664]**
2′	Five, rarely six, pairs of thoracic limbs, mostly of different morphology; not more than two pairs (III and IV) bearing numerous long filtering setae ..... **Anomopoda [p. 669]**
3(2)	Six pairs of thoracic limbs, abdomen well developed and segmented, postabdomen large ..... Haplopoda, Leptodoridae, one genus: ***Leptodora*** **[p. 720]**
3′	Four pairs of thoracic limbs, abdomen well developed or reduced, postabdomen reduced ..... **Onychopoda [p. 720]**

Diplostraca: Cladocera: Ctenopoda: Families

1	Both sexes antenna II two branched, upper antennal branch (exopodite) distal antennomere with lateral and apical setae; body not enclosed in transparent gelatinous envelope ..... **Sididae [p. 664]**
1′	Antenna II of females one branched, males two branched, distal antennomeres with only apical setae; body usually enclosed in transparent gelatinous envelope (Fig. 16.2.8 A) ..... Holopediidae, one species: *Holopedium gibberum* Zaddach, 1855 *sensu lato* [Widely distributed. In need of revision]

Cladocera: Ctenopoda: Sididae: Genera

1	Upper antennal branch (exopodite) with three antennomeres; carapace valves lacking long marginal setae and not forming a ventral inflexion directed inwards 2
1′	Upper antennal branch (exopodite) with two antennomeres; carapace valves bearing a varying number of long marginal setae and forming a ventral inflexion directed inwards 3
2(1)	Head oblong/oval with anchoring dorsal organs; rostrum present; postabdomen with lateral anal teeth ..... ***Sida*** **[p. 664]**
2′	Head triangular without anchoring organs; rostrum absent; postabdomen without lateral anal teeth (Figs. 16.2.8 B, C) ..... *Limnosida frontosa* Sars, 1862 [Northern Palearctic]
3(1)	Posterior and posterioventral valve margins with long plumose setae and especially long simple setae (often broken); postabdomen lateral anal teeth solitary 4
3′	Posterior and posterioventral valve margins without long setae, relatively short plumose setae may be present only on posterioventral valve margins; postabdomen lateral anal teeth if present, in clusters 5
4(3)	Upper antennal branch (exopodite) proximal antennomere with large lateral outgrowth bearing long setae; head ventral side with large broad foliar outgrowth (Figs. 16.2.8 D, E) ..... *Latona setifera* (O.F. Müller, 1776) [Holarctic]
4′	Upper antennal branch (exopodite) proximal antennomere without lateral outgrowth; head ventral side without large broad foliar outgrowth (Fig. 16.2.8 F) ..... *Latonopsis australis* Sars, 1888 *sensu lato* [China, Japan, South Korea, Turkmenistan, Uzbekistan. Oriental region. In need of revision]
5(3)	Female antenna I short, postabdomen without lateral anal teeth ..... ***Diaphanosoma*** **[p. 665]**
5′	Female antenna I long, postabdomen with clusters of anal teeth (Figs. 16.2.8 G, H) ..... *Pseudosida szalayi* (Daday, 1898) [extreme south of the Russian Far East South Korea. Oriental region.]

Cladocera: Sididae: *Sida*: Species

1	Rostrum relatively long (more than 20% of body length) and straight with apex directed backwards; postabdominal claw with proximal basal spine small, situated close to neighboring spine (Figs. 16.2.8 I–K) ..... *Sida crystallina* (O.F. Müller, 1776) [Palearctic]
1′	Rostrum relatively short (less then 20% of body length) with apex directed downwards and backwards; postabdominal claw with proximal basal spine relatively large and situated far from the neighboring spine (Figs. 16.2.8 L, M) ..... *Sida ortiva* Korovchinsky, 1979 [China, Eastern Russia. Oriental]

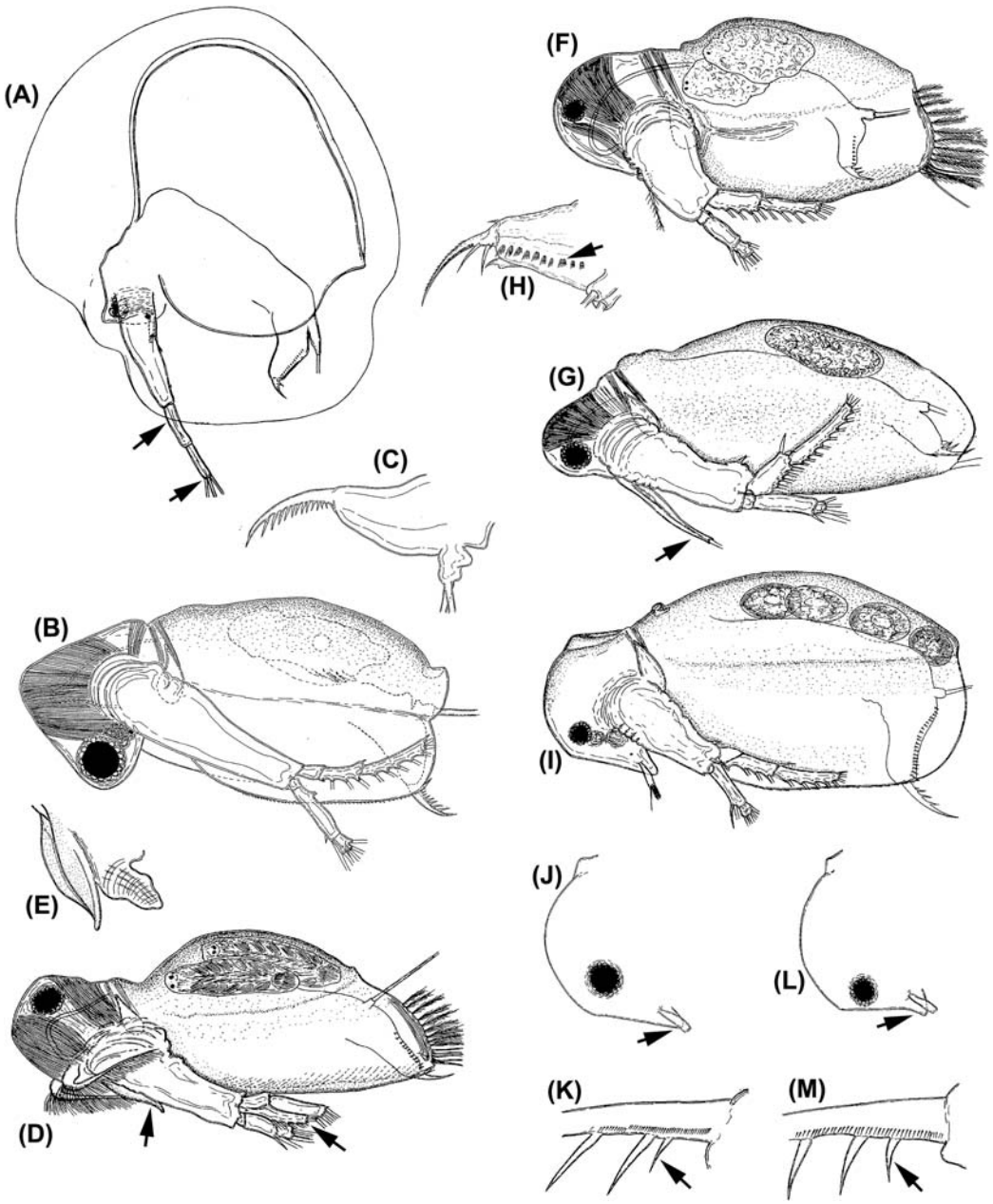


FIGURE 16.2.8 Representatives of Holopediidae (A) and Sididae (B–M): (A) *Holopedium gibberum*; (B and C) *Limnosida frontosa*, general view and postabdomen; (D and E) *Latona setifera*, general view and foliar outgrowth on ventral side of head; (F) *Latonopsis australis*; (G and H) *Pseudosida szalayi*, general view and postabdomen; (I–K) *Sida crystallina*, general view, head and postabdominal claw; (L and M) *Sida ortiva*, general view, head and postabdominal claw.

Cladocera: Sididae: *Diaphanosoma*: Species

1	Carapace ventral valve margins forming a narrow inflexion, smoothly connecting with the posterioventral margin	2
1′	Ventral valve margins form a wide, flap-shaped inflexion	14
2(1)	Denticles of posterioventral valve margin differ strongly in form and size: small intermediate denticles sit between large ones	3
2′	Denticles of posterioventral valve margin rather uniform (only dorsalmost and ventralmost are smaller)	5
3(2)	Antennal basipodite of females with a wide lanceolate spine distolaterally; posterioventral valve margin large denticles relatively close together, intermediate denticles relatively small or absent	4

3′ Antennal basipodite of females with very small acute spine; posterioventral valve margin large denticles relatively separated, intermediate denticles relatively large (Figs. 16.2.9 A, B) ..... *Diaphanosoma kizakiensis* Korovchinsky, 2012 [Japan: Lake Kizaki]

4(3) Head roundish-rectangular, dorsal margin slightly sloping anteriorly and smoothly joining anterior margin; eye 6%−10% of body length; posterioventral valve margins usually with 2−5 small denticles between large denticles; male copulatory appendages podiform (Figs. 16.2.9 C−H) ..... *Diaphanosoma brachyurum* (Lievin, 1848) [Needs revision. Palaearctic. Oriental]

4′ Head rectangular or slightly roundish-rectangular, eye 10%−18% of body length; posterioventral valve margin usually with 1−3 small denticles between large denticles or may be absent; male copulatory appendages conical with uneven distal margin (Figs. 16.2.9 I−L) ..... *Diaphanosoma amurensis* Korovchinsky & Sheveleva, 2009 [China, Japan, Eastern Russia]

5(2) Each valve margin with a posteriodorsal spine 6

5′ Each valve margin without a posteriodorsal spine 10

6(5) Head dorsum protruding with relatively small ventral eye 7

6′ Head rectangular, not protruding, with relatively large anterior or anterioventral eye 9

7(6) Head dorsum moderately protruding; second antennae not reaching or only slightly reaching beyond the valve posterior margin 8

7′ Head dorsum strongly protruding; second antennae reaching far beyond the valve posterior margin (Figs. 16.2.9 M−O) ..... *Diaphanosoma pseudodubium* Korovchinsky, 2000 [Eastern Russia]

8(7) Head 40%−45% of body length; valve posterioventral margins with 10−36 (usually 15−25) small denticles (Figs. 16.2.9 P−R) ..... *Diaphanosoma mongolianum* Ueno, 1938 [Palaearctic. Afrotopical]

8′ Head 34%−37% of body length; valve posterioventral margins with 25−60 (usually 30−50) small denticles (Figs. 16.2.9 S−U) ..... *Diaphanosoma lacustris* Kořinek, 1981 [Palaearctic, Afrotropical]

9(6) Head 38%−49% of body length; eye 10%−12% of body length; valve posterioventral margins with 8−21 (usually 9−15) large, wide denticles (Figs. 16.2.9 V−X) ..... *Diaphanosoma macrophthalma* Korovchinsky & Mirabdullaev, 1995 [China, Japan, Kazakhstan, Russia, Uzbekistan. Oriental]

9′ Head 32%−35% of body length; eye 6%−8% of body length; valve posterioventral margins with 12−22 (usually 13−18) small thin denticles (Figs. 16.2.10 A−C) ..... *Diaphanosoma dumonti* Korovchinsky, 1995 [China]

10(5) Valve posterioventral margins with numerous denticles and setules 11

10′ Valve posterioventral margin with numerous denticles but without setules between them (Figs. 16.2.10 D−F) ..... *Diaphanosoma chankensis* Ueno, 1939 [China (lakes of Lower Yangtze River), Russia (Lake Khanka)]

11(10) Head dorsum either slightly or not protruding; antennal basipodite distolateral end with small spine, valve posterior margin is relatively high 12

11′ Head dorsum strongly protruding; antennal basipodite distolateral end with thin seta; valve posterior margin very low, inconspicuously passing into ventral margin (Figs. 16.2.10 G, H) ..... *Diaphanosoma dubium* Manuilova, 1964 [China, Japan, Kazakhstan, Russia, South Korea, Uzbekistan. Oriental region]

12(11) Head dorsum not protruding, rectangular or roundish-rectangular; valve posterioventral margin denticles relatively wide, passing far along ventral margin; male copulatory appendages of male's podiform, expanding distally 13

12′ Head dorsum slightly protruding; valve posterioventral margin denticles relatively thin, not passing far along ventral margin; male copulatory appendages tubular, not distally expanded (Figs. 16.2.10 I, J) ..... *Diaphanosoma macedonicum* Korovchinsky & Petkovski, 2014 [Macedonia: Lakes Prespa and Dojran]

13(12) Head high, rectangular; valve posterioventral margin usually with not more than 25 (9−29 in general) relatively large denticles (Figs. 16.2.10 K, L) ..... *Diaphanosoma orghidani* Negrea, 1982 [needs revision. Palearctic. Oriental region]

13′ Head low, roundish-rectangular; valve posterioventral margin usually with more than 25 (24−38) small denticles (Figs. 16.2.10 M−P) ..... *Diaphanosoma orientalis* Korovchinsky, 1986 [Japan]

14(1) Head rectangular with strongly developed dorsum; carapace valves with ventral lamellar inflexion tapering distally and joining with posterioventral margin without depression (Figs. 16.2.10 Q, R) ..... *Diaphanosoma excisum* Sars, 1885 [Egypt, Pakistan, Uzbekistan.Afrotropical, Oriental]

14′ Head roundish-rectangular with weakly developed dorsum; carapace valves with ventral lamelliform inflexion cleft near junction with posterioventral margin (Figs. 16.2.10 S, T) ..... *Diaphanosoma sarsi* Richard, 1894 [Uzbekistan. Afrotropical, Oriental]

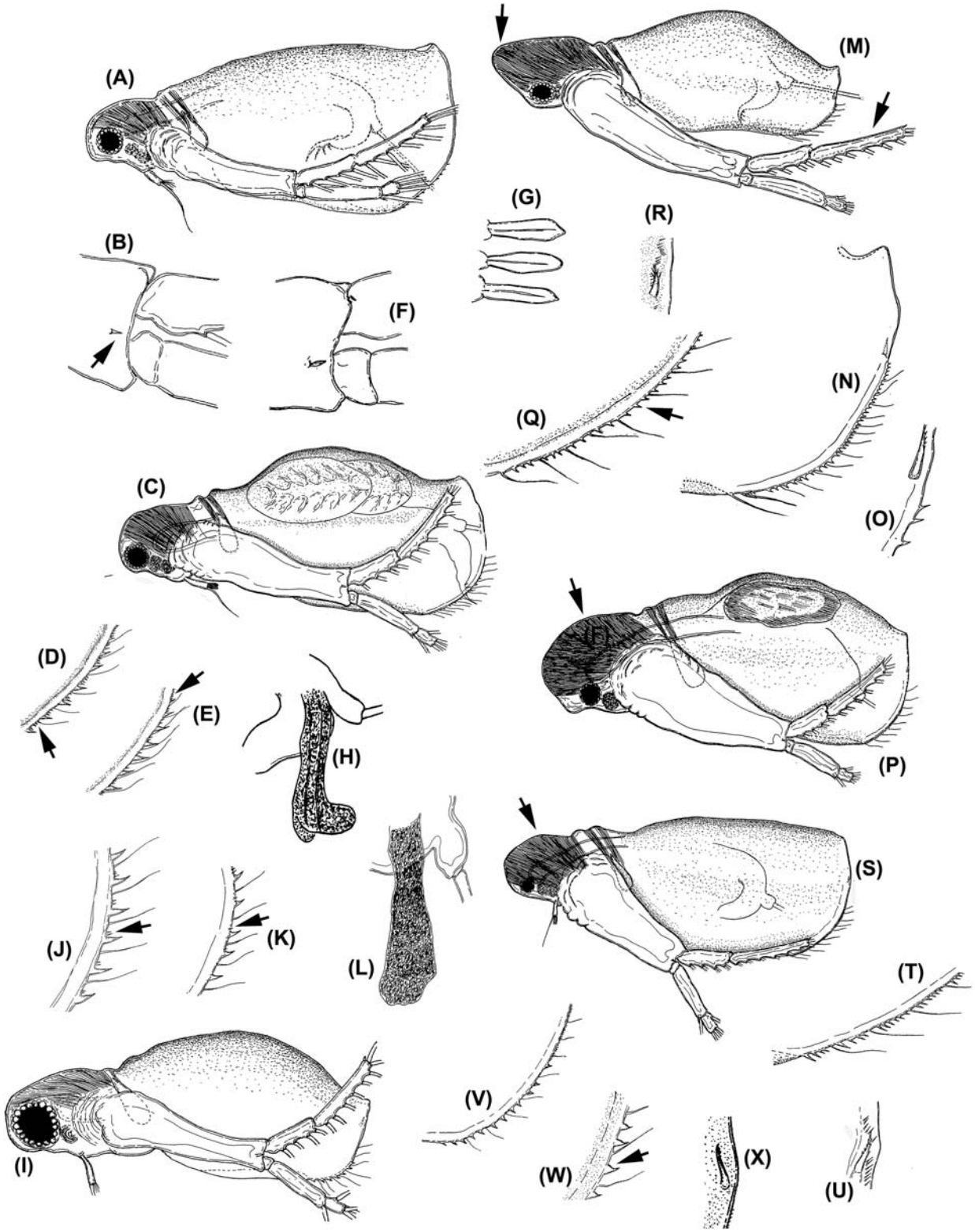


FIGURE 16.2.9 Representatives of *Diaphanosoma* (Sididae): (A and B) *Diaphanosoma kizakiensis*, general view and basal portion of antennal branches; (C–H) *Diaphanosoma brachyurum*, general view, armature of postero-ventral valve portion, basal portion of antennal branches, spine in distal portion of basal segment of antenna II, copulatory appandage of male; (I–L) *D. amurensis*, general view, armature of posteroventral valve portion, copulatory appandage of male; (M–O) *D. pseudodubium*, general view, armature of postero-ventral valve portion, spine on inner side of posterodorsal valve portion; (P–R) *D. mongolianum*, general view and spine on inner side of posterodorsal valve portion; (S–U) *D. lacustris*, general view, armature of postero-ventral valve portion and spine on inner side of posterodorsal valve portion; (V–X) *Diaphanosoma macrophthalma*, armature of postero-ventral valve portion and spine on inner side of posterodorsal valve portion.

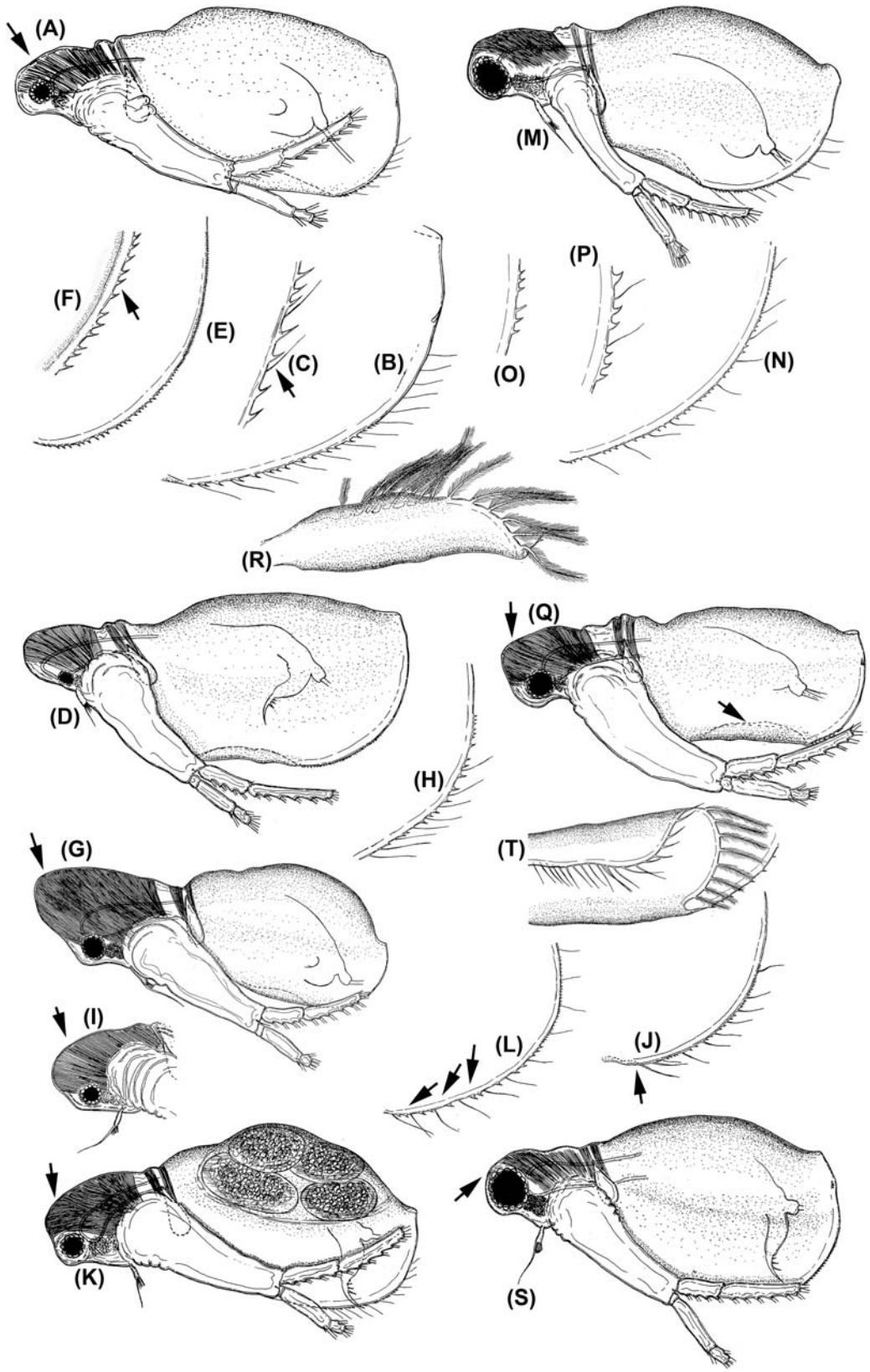


FIGURE 16.2.10 Representatives of *Diaphanosoma* (Sididae): (A–C) *Diaphanosoma dumonti*, general view and armature of posteroventral portion of valve; (D–F) *Diaphanosoma chankensis*, general view and armature of posteroventral portion of valve; (G and H) *Diaphanosoma dubium*, general view and armature of posteroventral portion of valve; (I and J) *D. macedonicum*, general view and armature of posteroventral portion of valve; (K and L) *Diaphanosoma orghidani*, general view and armature of posteroventral portion of valve; (M–P) *Diaphanosoma orientalis,* general view and armature of posteroventral portion of valve; (Q and R) *Diaphanosoma excisum*, general view and ventral flap of valve; (S and T) *Diaphanosoma sarsi*, general view and ventral flap of valve.

Branchiopoda: Anomopoda: Families

1 Antenna I of female not fused with rostrum, or, if fused, it is short and not forming a prosbosciform structure 2

1′ Antenna I of females long, fused with rostrum, prosbosciform ..... **Bosminidae [p. 690]**

2(1) Antenna II short, with both branches bearing three antennomeres 3

2′ Antenna II relatively long, exopod of four antennomeres (proximal antennomere usually small!), endopod of three antennomeres 4

3(2) Postabdomen wide, with serrate preanal margin; thoracic limbs III–IV exopodites with 8–10 setae, females with numerous eggs ..... Eurycercidae, one genus: ***Eurycercus*** **[p. 690]**

3′ Preanal margin not serrate, thoracic limbs III–IV exopodites with 7 or less setae, females with 1–2 eggs only ..... **Chydoridae [p. 690]**

4(2) Antenna I of females long 5

4′ Antenna I of female short ..... **Daphniidae [p. 669]**

5(4) Antenna I located on head anterioventral angle 6

5′ Antenna I on head ventral surface, relatively far from its anterioventral angle 8

6(5) Postabdomen wide, not tapering distally, anus located distally or subdistally 7

6′ Postabdomen conically tapering distally, anus opens in middle of dorsal margin ..... Ophryoxidae, one genus: ***Ophryoxus*** **[p. 685]**

7(6) Six pairs of thoracic limbs, limbs IV–V with large exopodites (Figs. 16.2.23 A, B) ..... Acantholeberidae, one species *Acantholeberis curvirostris* (O.F. Müller, 1776) [Palaearctic]

7′ Five pairs of thoracic limbs, exopodites on all limbs small ..... **Macrothricidae [p. 686]**

8(6) Antenna I of one antennomere, valve ventral margin setae short or absent ..... **Moinidae [p. 682]**

8′ Antenna I of two antennomeres, valve ventral margin setae large, plumose ..... Ilyocryptidae, one genus: ***Ilyocryptus*** **[p. 682]**

Branchiopoda: Anomopoda: Daphniidae: Genera

1 Valve ventral margin straight, posterioventral angle with a strong spine (mucro) 2

1′ Valve ventral margin convex, posteriodorsal angle with a strong spine or spine absent 3

2(1) Rostrum long and pointed, head shield posterior portion bearing a large fenestra (“head pore”) ..... ***Megafenestra*** **[p. 678]**

2′ Rostrum short and blunt, head shield without a fenestra ..... ***Scapholeberis*** **[p. 678]**

3(1) Female antenna I not fused to head, carapace without a caudal spine (may have a triangular projection), ephippium with a single egg 4

3′ Female antenna I fused to head, carapace with a caudal spine, ephippium usually with two eggs ..... ***Daphnia*** **[p. 671]**

4 Head normally without a rostrum, postabdomen of moderate width, without anal sulcus ..... ***Ceriodaphnia*** **[p. 669]**

4′ Head with a rostrum, postabdomen specially wide, with anal sulcus ..... ***Simocephalus*** **[p. 678]**

Branchiopoda: Anomopoda: Daphniidae: *Ceriodaphnia*: Species

1 Rostrum absent 2

1′ Rostrum present (Fig. 16.2.11 A) ..... *Ceriodaphnia cornuta* Sars, 1885 species group [in subtropics]

2(1) Head and valves without denticles, or present only on head anterior portion 3

2′ Head and valves with numerous small denticles (Figs. 16.2.11 B, C) ..... *Ceriodaphnia setosa* Matile, 1890 [Widespread]

3(2) Postabdomen dorsal margin without a depression near anus 4

3′ Postabdomen dorsal margin with a depression near anus (Figs. 16.2.11 D, E) ..... *Ceriodaphnia megops* Sars, 1862 [Europe, Russia]

4(3) Postabominal claw concave margin with some denticles larger than others 5

4′ Postabominal claw concave margin with denticles fine, and similar in size 7

5(4) Postabdominal claw with 3–7 larger denticles 6

5′ Postabdominal claw with about 20 larger denticles (Fig. 16.2.11 F) ..... *Ceriodaphnia dubia* Richard, 1894 species group [Cosmopolitan. Needs revision]

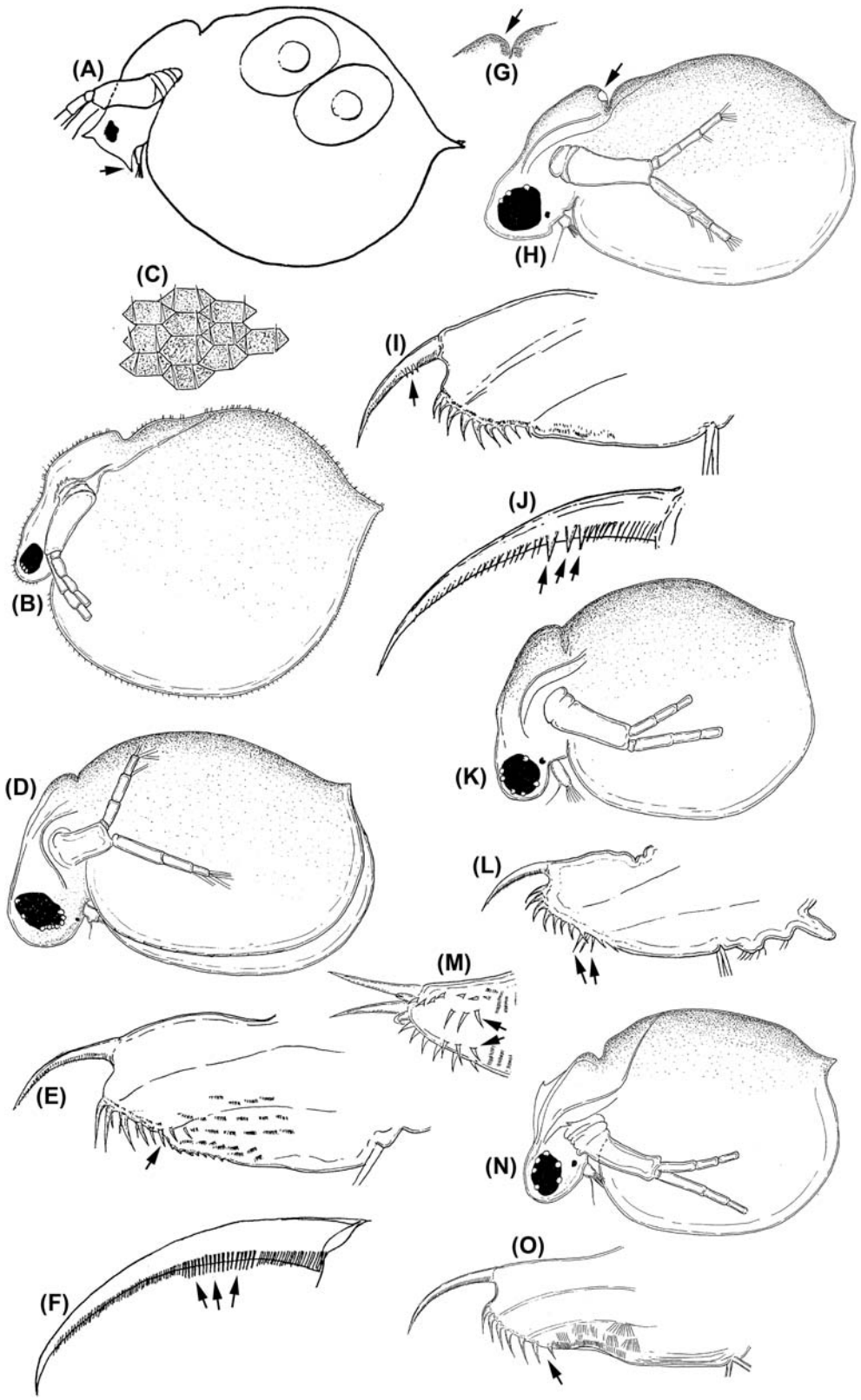


FIGURE 16.2.11 Representatives of *Ceriodaphnia* (Daphniidae): (A) *Ceriodaphnia cornuta*; (B and C) *Ceriodaphnia* setosa, general view and denticles on valves; (D and E) *Ceriodaphnia megops*, general view and postabdomen; (F) *Ceriodaphnia dubia*, postabdominal claw; (G) *Ceriodaphnia turkestanica*, head pore region; (H–J) *Ceriodaphnia reticulata*, general view, postabdomen and postabdominal claw; (K–M) *Ceriodaphnia pulchella*, general view and postabdomen in lateral and dorsal view; (N and O) *Ceriodaphnia quadrangula*, general view and postabdomen.

6(5) Dorsal head fenestra absent (Fig. 16.2.11 G) ..... *Ceriodaphnia turkestanica* Berner & Rakhmatullaeva, 2001 [Central Asia]

6′ Dorsal head fenestra present (Figs. 16.2.11 H–J) ..... *Ceriodaphnia reticulata* (Jurine, 1820) species group [Cosmopolitan. Needs revision]

7(4) Postabdomen maximum width in proximal portion 8

7′ Postabdomen maximum width in middle portion 9

8(7) Proximal anal denticles with additional denticles in between (Figs. 16.2.11 K–M) .... *Ceriodaphnia pulchella* Sars, 1862 species group (Holarctic. Needs revision)

8′ Proximal anal denticles without additional denticles (Figs. 16.2.11 N, O) ..... *Ceriodaphnia quadrangula* (O.F. Mueller, 1785) species group (Holarctic. Needs revision)

9(7) Head anterior portion without denticles (Figs. 16.2.12 A, B) ..... *Ceriodaphnia laticaudata* P.E. Müller, 1867 species group (Holarctic)

9′ Head anterior portion with small denticles (Fig. 16.2.12 C) ..... *Ceriodaphnia rotunda* Sars, 1862 (Palaearctic)

Branchiopoda: Anomopoda: Daphniidae: *Daphnia*: Subgenera

1 Fornices widely rounded, head shield posterior portion projects between anterior portions of valves; ephippium with egg axes perpendicular or subperpendicular to dorsal margin (Figs. 16.2.12 D, E) ..... ***Daphnia* s.str. [p. 672]**

1′ Fornices projecting, triangular, with rounded or pointed tips, and/or carapace dorsal margin with anterior projection jutting into head shield; ephippium with egg axes parallel or subparallel to dorsal margin (Figs. 16.2.12 F, G) ..... ***Daphnia* (*Ctenodaphnia*) [p. 676]**

Branchiopoda: Anomopoda: Daphniidae: *Daphnia: Daphnia* (*Daphnia*): Species

1 Postabdominal claw pecten with two lateral surface spinules significantly larger than pecten three (distal) spinules (only in few populations spinules in pecten two greatly varying in size); antenna I flagellum (additional male seta) 2–4 times longer than aesthetascs 2

1′ Postabdominal claw pecten two and three with lateral spinules of similar size; antenna I flagellum (additional male seta) less then two times longer than aesthetascs (*Daphnia longispina* species group) 11

2(1) Antenna I rudimentary or absent (*Daphnia* (*Daphnia*) *curvirostris* species group) 3

2′ Antenna I normal (*Daphnia* (*Daphnia*) *pulex* species group) 6

3 Adult female head lacking crest 4

3′ Adult female head with crest (Figs. 16.2.14 D–G) ..... *Daphnia* (*Daphnia*) *hrbaceki* Juračka, Kořínek & Petrusek, 2010 [Czech Republic]

4(3) Head posterior marginal projection low, with fine reticulation, not separated from labrum by a depression 5

4′ Head posterior marginal projection dorsal to antenna I, large, heavily reticulated, separated from labrum by a deep depression (Figs. 16.2.14 H–J) ..... *Daphnia* (*Daphnia*) *sinevi* Kotov, Isida & Taylor, 2006 [Russia]

5(4) Female rostrum long; abdominal proximal projection longer than postabdominal claw; male antenna I sensory seta reaches flagellum projection apex (Figs. 16.2.14 K–N) ..... *Daphnia* (*Daphnia*) *curvirostris* Eylmann, 1887 [Palaearctic]

5′ Female rostrum short; abdominal proximal projection shorter than postabdominal claw; male antenna I sensory seta does not reach flagellum projection apex (Figs. 16.2.14 O–R) ..... *Daphnia* (*Daphnia*) *tanakai* Ishida, Kotov & Taylor, 2006 [Japan]

6(2) Female valve ventromedial margin lacking long, plumose setae 7

6′ Female valve ventromedial margin with long, plumose setae (Figs. 16.2.15 A, B) ..... *Daphnia* (*Daphnia*) *obtusa* Kurz, 1874 species group [Cosmopolitan]

7(6) Not as below 8

7′ Ocellus very small; female body length <1.5 mm, normally <1.2 mm; rostrum very short and wide (Fig. 16.2.15 C) ..... *Daphnia* (*Daphnia*) *parvula* Fordyce, 1901 [Probably introduced: western Europe. Nearctic]

8(7) Female body length >1.5 mm; male seta (flagellum) without a spatulate apex 9

8′ Female body length <1.5 mm; male seta (flagellum) with apex spatulate (Figs. 16.2.15 D, E) ..... *Daphnia* (*Daphnia*) *ambigua* Scourfield, 1947 [Probably introduced: western Europe. Nearctic]

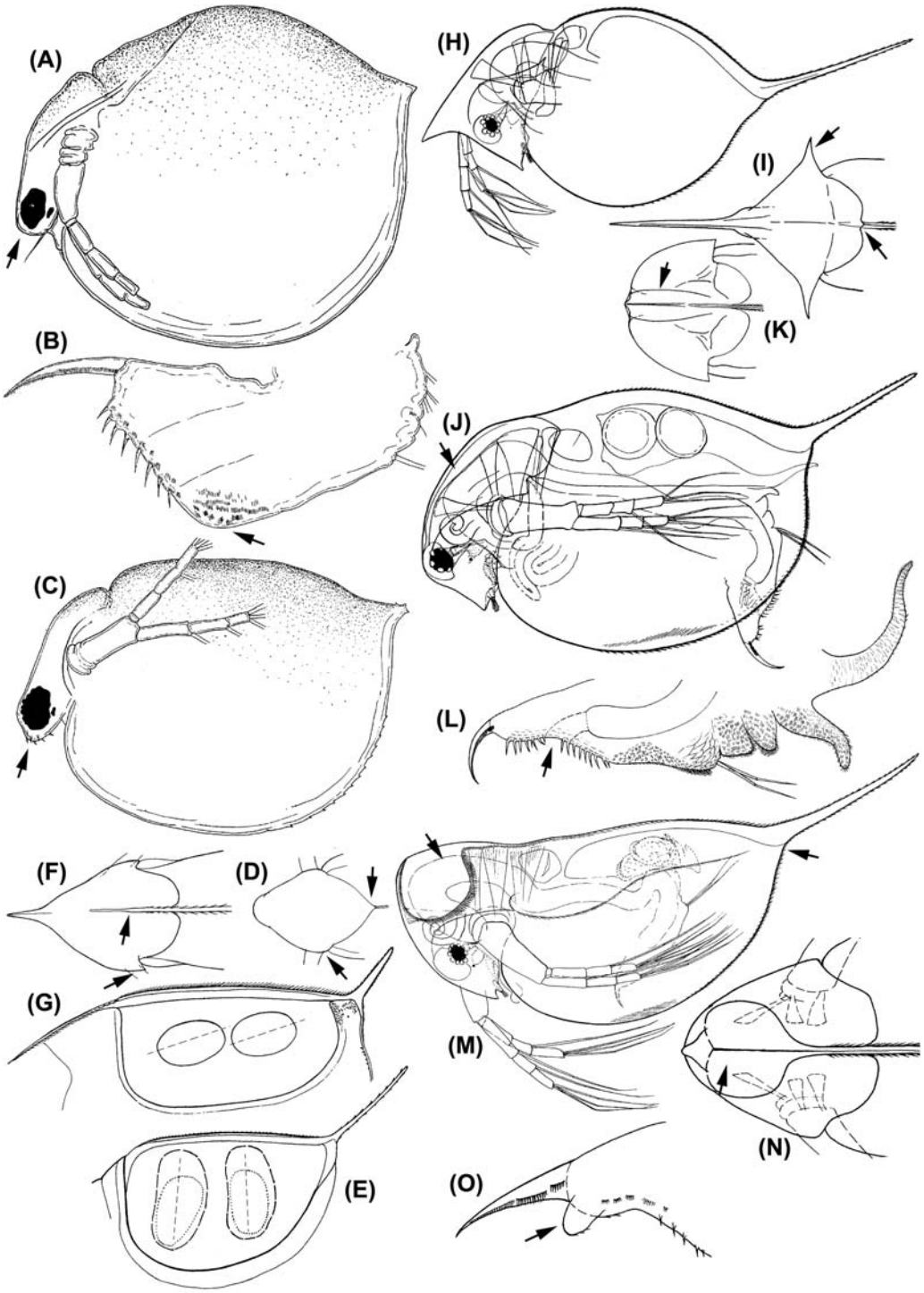


FIGURE 16.2.12 Representatives of Daphniidae: (A and B) *Ceriodaphnia laticaudata*, general view and postabdomen; (C) *Ceriodaphnia rotunda*; (D and E) diagnostic features of subgenus *Daphnia* s.str., head shield and ephippium; (F and G) diagnostic features of subgenus *Daphnia* (*Ctenodaphnia*), head shield and ephippium; (H and I) *Daphnia* (*Ctenodaphnia*) *lumholtzi*, general view and head shield; (J–L) *Daphnia* (*Ctenodaphnia*) *magna*, general view, head shield and postabdomen; (M–O) *Daphnia* (*Ctenodaphnia*) *atkinsoni*, general view, head shield and male postabdomen.

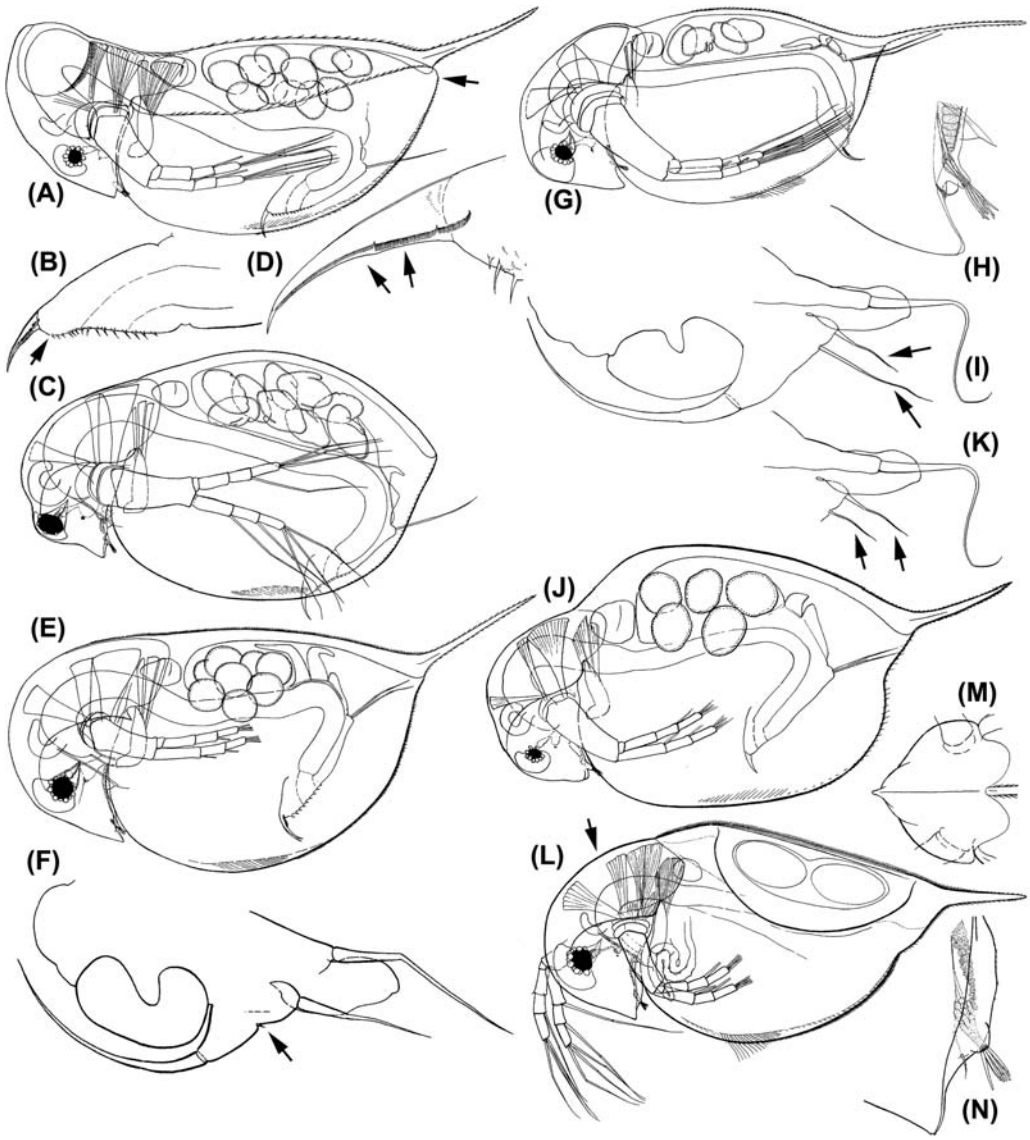


FIGURE 16.2.13 Representatives of *Daphnia* (*Ctenodaphnia*) (Daphniidae): (A and B) *Daphnia* (*Ctenodaphnia*) *triquetra*, general view and male postabdomen; (C and D) *Daphnia* (*Ctenodaphnia*) *tibetana*, general view and postabdominal claw; (E and F) *Daphnia* (*Ctenodaphnia*) *similis*, general view and limb V; (G–I) *Daphnia* (*Ctenodaphnia*) *fusca*, general view, rostrum, and limb V; (J and K) *Daphnia* (*Ctenodaphnia*) *mediterranea*, general view and limb V; (L–N) *Daphnia* (*Ctenodaphnia*) *hispanica*, general view, antenna I and head shield.

9(8)	Carapace valve ventral margin with more than half covered in denticles; male abdominal proximal process short 10
9′	Carapace valve ventral margin with less than half covered in denticles; male abdominal proximal process long (Figs. 16.2.15 F–H) ..... *Daphnia* (*Daphnia*) *pulex* Leydig, 1860 species group [Cosmopolitan. Needs revision]
10(9)	Head anteriodorsal portion alsant, lacking dorsal crest; male flagellum with apex spatulate (Figs. 16.2.15 I–K) ..... *Daphnia* (*Daphnia*) *middendorffiana* Fischer, 1851 [Arctic]
10′	Head anteriodorsal portion widely rounded, dorsal crest present; male flagellum with apex not spatulate (Figs. 16.2.15 L, M) ..... *Daphnia* (*Daphnia*) *pulicaria* Forbes, 1893 species group [Holarctic. Needs revision]
11(1)	Antenna II endopod (with three antennomeres) with proximal antennomere seta shorter than a sum of the lengths of the setae on the two distal antennomeres, or absent 12

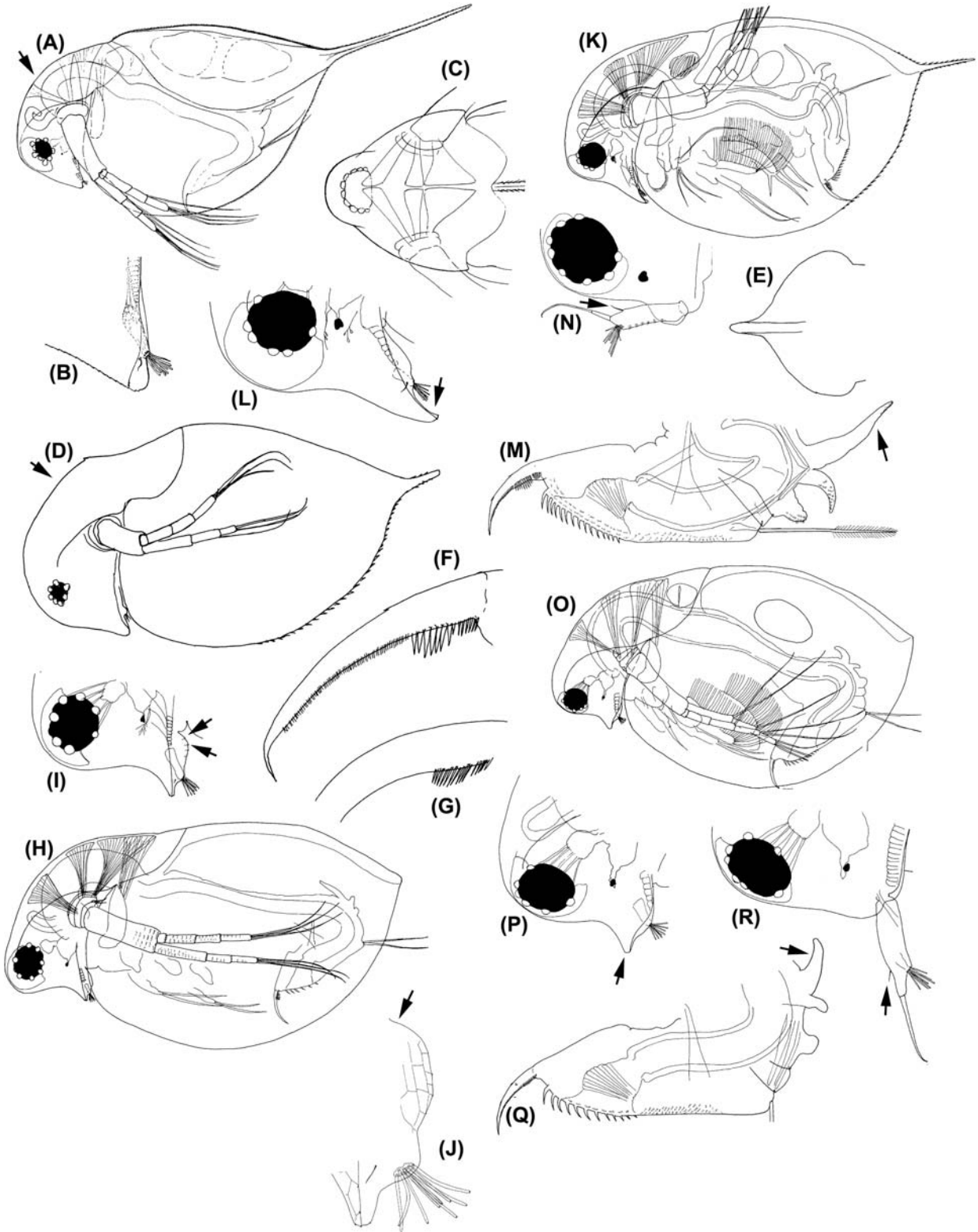


FIGURE 16.2.14 Representatives of *Daphnia* (*Ctenodaphnia*) (A–C) and *Daphnia* (*Daphnia*) (D–R) (Daphniidae): (A–C) *Daphnia* (*Ctenodaphnia*) *chevreuxi*, general view, rostrum and head shield; (D–G) *Daphnia* (*Daphnia*) *hrbaceki,* general view, head in dorsal view, postabdominal claw of two different females; (H–J) *Daphnia sinevi*, general view, head and antenna I; (K–N) *Daphnia* (*Daphnia*) *curvirostris*, general view, head, postabdomen and head of male; (O–R) *Daphnia* (*Daphnia*) *tanakai*, general view, head, postabdomen and head of male.

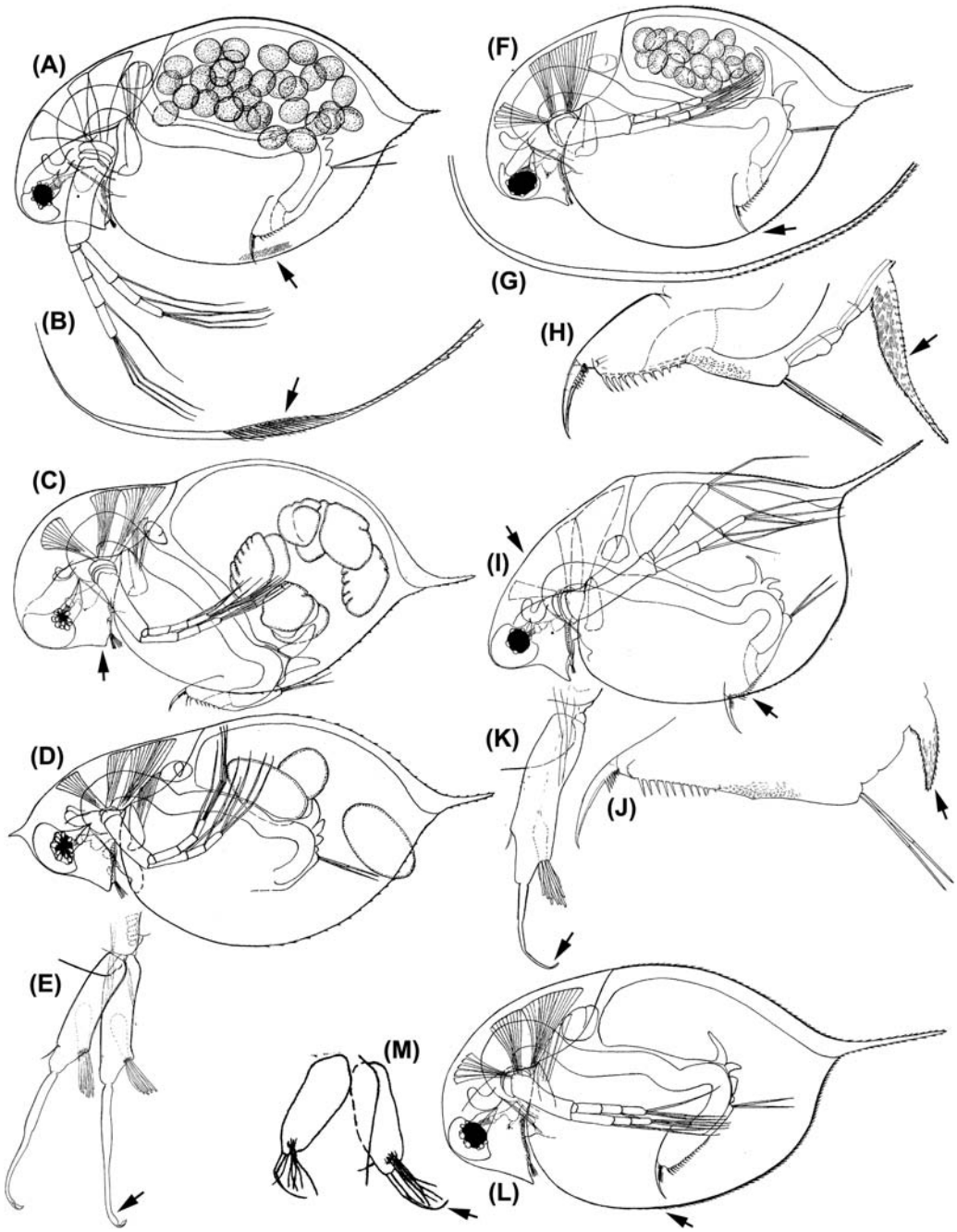


FIGURE 16.2.15 Representatives of *Daphnia* (*Daphnia*) (Daphniidae): (A and B) *Daphnia* (*Daphnia*) *obtusa*, general view and ventral margin of valve; (C) *Daphnia* (*Daphnia*) *parvula*; (D and E) *Daphnia* (*Daphnia*) *ambigua*, general view of female and antennae I of male; (F–H) *Daphnia* (*Daphnia*) *pulex*, general view, ventral margin of valve and male postabdomen; (I–K) *Daphnia* (*Daphnia*) *middendorffiana*, general view, male postabdomen and antenna I; (L and M) *Daphnia* (*Daphnia*) *pulicaria*, female general view and male antennae I.

11′	Antenna II endopod (with three antennomeres) with proximal antennomere seta longer than a sum of lengths of the setae on the two distal antennomeres 13
12(11)	Antenna II endopod, proximal antennomere with a short seta present (Figs. 16.2.16 A, B) .... *Daphnia* (*Daphnia*) *longiremis* Sars, 1862 [Northern Palaearctic]
12′	Antenna II endopod, proximal antennomere without a seta (Figs. 16.2.16 C, D) ..... *Daphnia* (*Daphnia*) *cristata* Sars, 1862 [Northern Palaearctic]
13(11)	Ocellus present; head posterior margin with aesthetascs not protruding from rostrum apex 14
13′	Ocellus usually absent; head posterior margin with aesthetascs on rostrum apex (Figs. 16.2.16 E–G) .... *Daphnia* (*Daphnia*) *cucullata* Sars, 1862 [Palaearctic]
14(13)	Females head posterior face either lacking a medial keel (prominence between aesthetascs), or with a low keel with maximum breadth at middle; helmet absent or rounded (Figs. 16.2.16 H, I) ..... *Daphnia* (*Daphnia*) *longispina* O.F. Müller, 1785 species group [Cosmopolitan. Needs revision]
14′	Females head posterior face with a high medial keel, with maximum breadth near rostrum; frequently females have helmet pointed (Figs. 16.2.16 J, K) ..... *Daphnia* (*Daphnia*) *galeata* Sars, 1864 [Palaearctic]

Branchiopoda: Anomopoda: Daphniidae: *Daphnia: Daphnia* (*Ctenodaphnia*): Species

1	Head shield with posterior incision; fornices as short triangular (or, rarely, rounded) projections 2
1′	Head shield without posterior incision; fornices spiniform (Figs. 16.2.12 H, I) .... *Daphnia* (*Ctenodaphnia*) *lumholtzi* Sars, 1885 species group [Central Asia, Iran, Russia, China]
2(1)	Head shield between medial keel and fornix without additional ridges; female postabdomen near anus without a deep sulcus 3
2′	Head shield between medial keel and fornix with additional ridges on each side between medial keel and fornix; female postabdomen near anus a deep sulcus (Figs. 16.2.12 J–L) ..... *Daphnia* (*Ctenodaphnia*) *magna* Straus, 1820 species group [Palaearctic]
3(2)	Carapace medial keel deeply penetrates head shield, expanding as a head plate 4
3′	No head plate 5
4(3)	Carapace ventral margin near caudal spine without a projection; male gonopores on large projection (Figs. 16.2.12 M–O) .... *Daphnia* (*Ctenodaphnia*) *atkinsoni* Baird, 1859 species group [Europe]
4′	Carapace ventral margin near caudal spine with a projection; male gonopores on very small projections (Figs. 16.2.13 A, B) .... *Daphnia* (*Ctenodaphnia*) *triquetra* Sars, 1903 [Southern Europe, Kazakhstan, Mongolia]
5(3)	Postabdomen first and second pectens with lateral setules significantly larger than those of third pecten 6
5′	Postabdomen pectens with setules all of similar size (Figs. 16.2.13 C, D) ..... *Daphnia* (*Ctenodaphnia*) *tibetana* Sars, 1903 [Central Asia, China, Mongolia]
6(5)	Limb V exopod with two large setae directed distally 7
6′	Limb V exopod with only one large seta directed distally, second seta rudimentary or absent (Figs. 16.2.13 E, F) .... *Daphnia* (*Ctenodaphnia*) *similis* Claus, 1876 species group [southern Palaearctic]
7(6)	Female antenna I a distinct short cylindrical projection 8
7′	Female antenna I rudimentary 9
8(7)	Body pigmented; exopod V proximal seta longer than distal seta (Figs. 16.2.13 G–I) .... *Daphnia* (*Ctenodaphnia*) *fusca* Gurney, 1907 [central Asia]
8′	Body not pigmented; exopod V proximal seta shorter than distal seta (Figs. 16.2.13 J, K) .... *Daphnia* (*Ctenodaphnia*) *mediterranea* Alonso, 1985 [Mediterranean]
9(7)	Head with medial crest; ephippium occupies only a part of carapace dorsal portion (Figs. 16.2.13 L–N) .... *Daphnia* (*Ctenodaphnia*) *hispanica* Glagolev & Alonso, 1990 [Spain]
9′	Head without medial crest; ephippium occupies all carapace dorsal portion (Figs. 16.2.14 A–C) .... *Daphnia* (*Ctenodaphnia*) *chevreuxi* Richard, 1896 species group [Mediterranean. Needs revision]

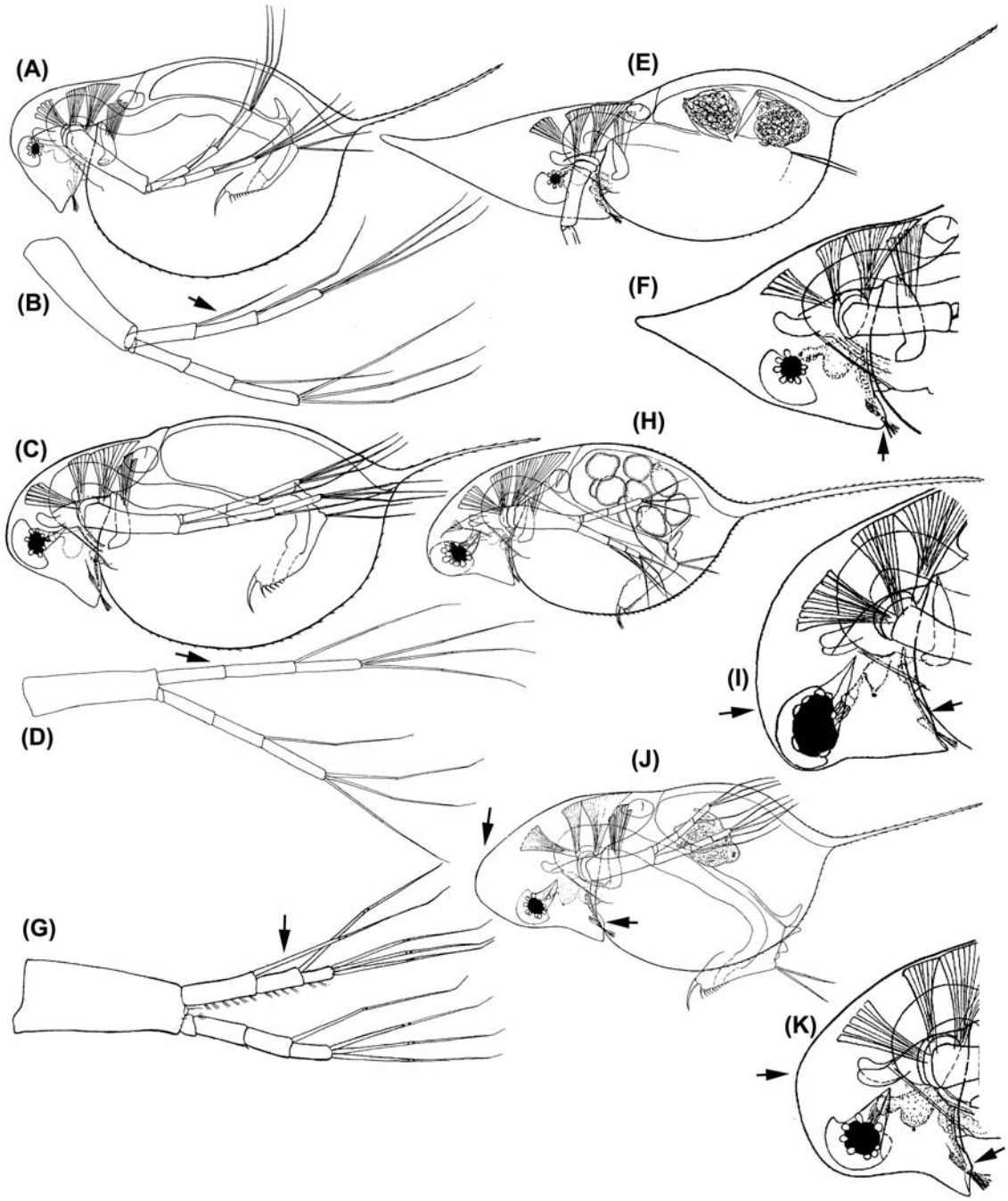


FIGURE 16.2.16 Representatives of *Daphnia* (*Daphnia*) (Daphniidae): (A and B) *Daphnia* (*Daphnia*) *longiremis*, general view and antenna II; (C and D) *Daphnia* (*Daphnia*) *cristata*, general view and antenna II; (E–G) *Daphnia* (*Daphnia*) *cucullata*, general view, head and antenna II; (H and I) *Daphnia* (*Daphnia*) *longispina*, general view and head; (J and K), *Daphnia* (*Daphnia*) *galeata*, general view and head.

Branchiopoda: Anomopoda: Daphniidae: *Megafenestra*: Species

1 Carapace ventral margin with anterior third with separated setules, posterior two thirds with close set setules (Figs. 16.2.17 A, B) ..... *Megafenestra aurita* (Fischer, 1849) [Palaearctic]

1′ Carapace ventral margin with separated setules, less than half with close set setules (Fig. 16.2.17 C) ..... *Megafenestra nasuta* (Birge, 1879) [Russia]

Branchiopoda: Anomopoda: Daphniidae: *Scapholeberis*: Species

1 Head and valves without spinules 2

1′ Head and valves covered with spinules and other minute, pointed projections (Fig. 16.2.17 D) ... *Scapholeberis erinaceus* Daday, 1903 [central Europe, Kazakhstan, Siberia]

2(1) Rostrum anterior rectilinear in both sexes; postabdominal claw concave (dorsal) margin with all setules of subequal size 3

2′ Rostrum anterior trilobate or triangular in both sexes; postabdominal claw concave (dorsal) margin with 2–5 proximal setules significantly larger than others 4

3(2) Head large; antenna I not protruding beyond anterior rostrum margin (Figs. 16.2.17 E–G) ..... *Scapholeberis mucronata* (O.F. Müller, 1776) [Palaearctic]

3′ Head small; antenna I protruding beyond rostrum anterior margin (Fig. 16.2.17 H) ..... *Scapholeberis microcephala* Sars, 1890 [northern Palaearctic]

4(2) Rostrum anterior triangular; between eye and rostrum apex are paired lateral depressions; head behind antenna I insertion with grooves (Figs. 16.2.17 I, J) ..... *Scapholeberis rammneri* Dumont & Pensaert, 1983 [central and southern Palaearctic]

4′ Rostrum anterior trilobed; head without depressions or grooves (Fig. 16.2.17 K) ..... *Scapholeberis kingii* Sars, 1888 species group [Southern Palaearctic. Oriental. Needs revision]

Branchiopoda: Anomopoda: Daphniidae: *Simocephalus*: Species

1 Dorsal margin of postabdominal claw with monotonous row of setules, lacking any denticles 2

1′ Dorsal margin of postabdominal claw with a proximal or a distal row of denticles 6

2(1) No teeth near postabdomen dorsodistal angle 3

2′ Teeth present near postabdomen dorsodistal angle 4

3 Valves without lateral projections (Figs. 16.2.18 A–E) ..... *Simocephalus* (*Aquipiculus*) *heilongjiangensis* Shi & Shi, 1994 [central Asia, China. Oriental and Afrotropical]

3′ Valves with lateral projections (Fig. 16.2.18 F) ..... *Simocephalus* (*Aquipiculus*) *lusaticus* Herr, 1917 [China, Europe]

4(2) Posteriodorsal prominence relatively high 5

4′ Posteriodorsal prominence very low or absent (Figs. 16.2.18 G, H) ..... *Simocephalus* (*Simocephalus*) *vetulus* (O.F. Müller, 1776) [Europe, eastern distribution unclear]

5(4) Posteriodorsal valve prominence wide; dorsal valve margin protruding posteriorly (Fig. 16.2.18 I) ..... *Simocephalus* (*Simocephalus*) *mixtus* Sars, 1903 [Palearctic. Oriental, Australia, Nearctic]

5′ Posteriodorsal valve prominence narrow; dorsal valve margin not protruding posteriorly (Fig. 16.2.18 J) ..... *Simocephalus* (*Simocephalus*) *vetuloides* Sars, 1898 [China, Russia]

6(3) Head lacking anterior denticles 7

6′ Denticles on front of head (Figs. 16.2.18 K, L) ..... *Simocephalus* (*Coronocephalus*) *serrulatus* (Koch, 1841) [cosmopolitan]

7(6) Front of head rounded 8

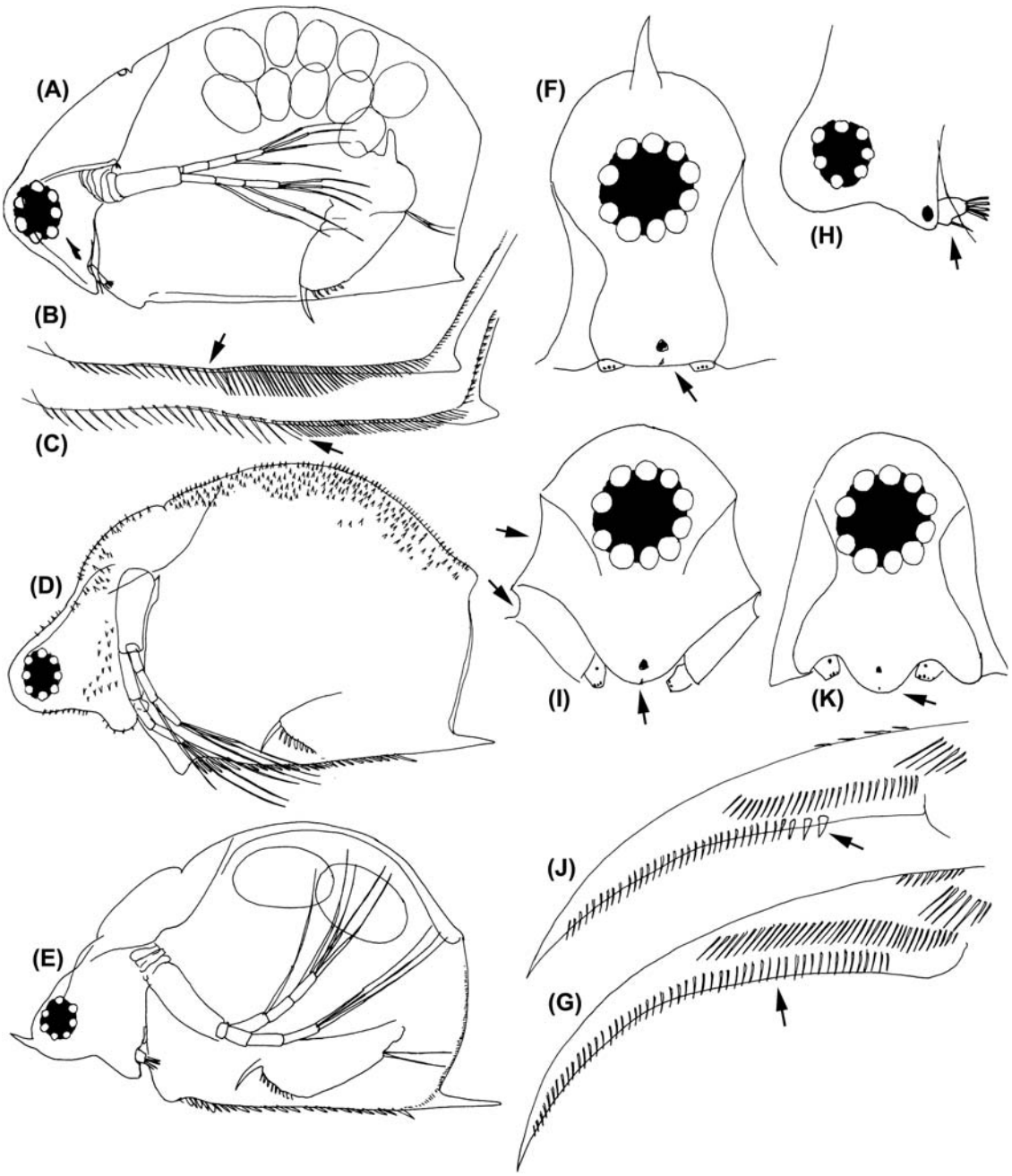


FIGURE 16.2.17 Representatives of Daphniidae: (A and B) *Megafenestra aurita*, general view and ventral portion of valve. (C) *Megafenestra nasuta*, ventral portion of valve; (D) *Scapholeberis erinaceus*; (E–G) *Scapholeberis mucronata*, general view, head in ventral view and postabdominal claw; (H) *Scapholeberis microcephala*, head in lateral view; (I and J) *Scapholeberis rammneri*, head in ventral view and postabdiominal claw; (K), *Scapholeberis kingii*, head in lateral view.

7′	Front of head projecting (Figs. 16.2.18 M, N) ..... *Simocephalus* (*Echinocaudus*) *acutirostratus* (King, 1853) [Oriental region]	
8(7)	Postabdominal claw with about 30 thin proximal denticles (Fig. 16.2.18 O) ..... *Simocephalus* (*Echinocaudus*) *congener* (Koch, 1841) [Palaearctic]	
8′	Postabdominal claw with about 15 large, relatively thick proximal denticles (Fig. 16.2.18 P) ..... *Simocephalus* (*Echinocaudus*) *exspinosus* (De Geer, 1778) [Palaearctic]	

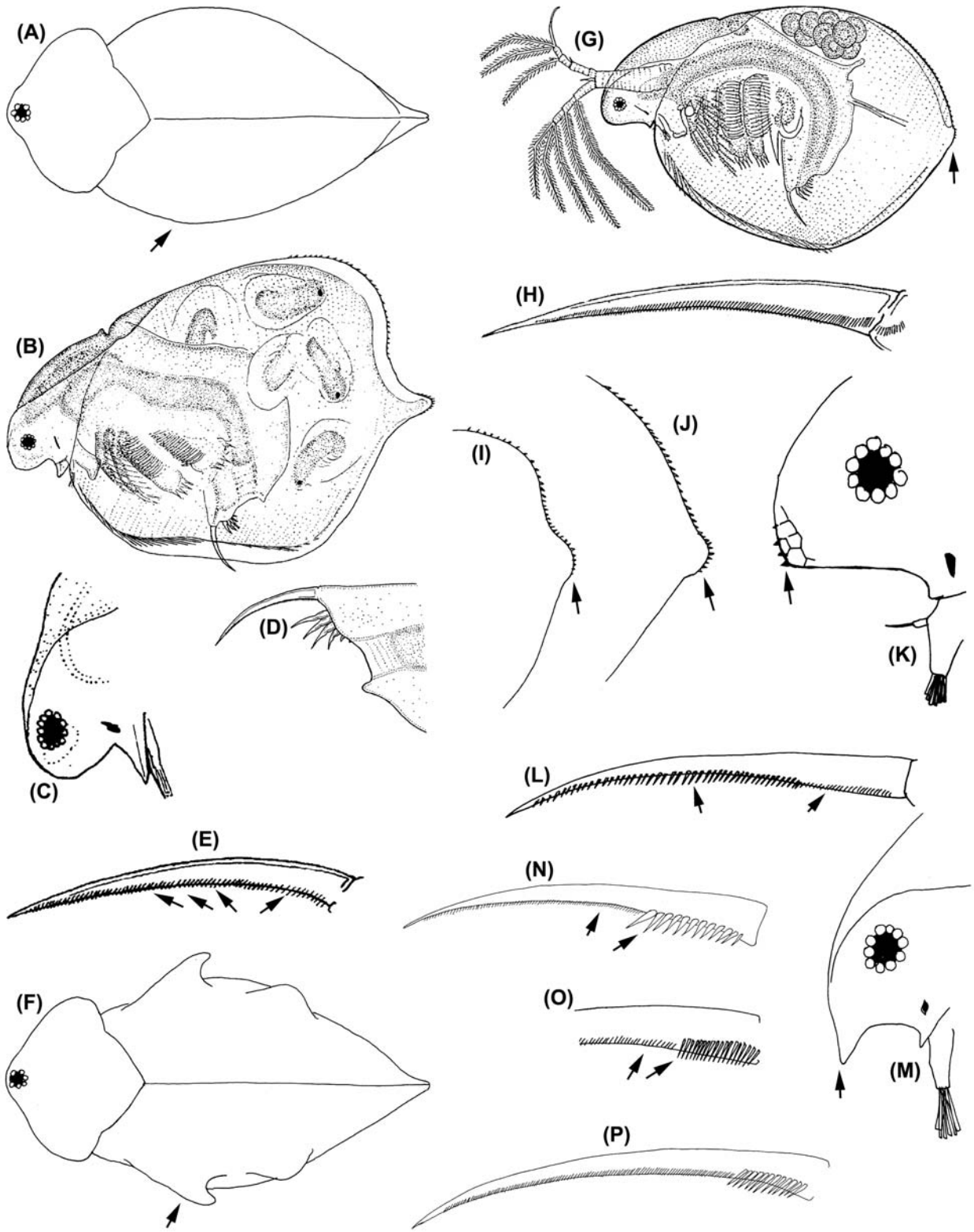


FIGURE 16.2.18 Representatives of *Simocephalus* (Daphniidae): (A–E) *Simocephalus* (*Aquipiculus*) *heilongjiangensis*, dorsal and lateral view, head postabdomen and postabdominal claw; (F) *Simocephalus* (*Aquipiculus*) *lusaticus*, dorsal view; (G and H) *Simocephalus* (*Simocephalus*) *vetulus*, lateral view and postabdominal claw; (I) *Simocephalus* (*Simocephalus*) *mixtus*, dorsal margin of valves; (J) *Simocephalus* (*Simocephalus*) *vetuloides*, dorsal margin of valves; (K and L) *Simocephalus* (*Coronocephalus*) *serrulatus*, head and postabdominal claw; (M and N) *Simocephalus* (*Echinocaudus*) *acutirostratus*, head and postabdominal claw; (O) *Simocephalus* (*Echinocaudus*) *congener*, postabdominal claw; (P) *Simocephalus* (*Echinocaudus*) *exspinosus*, postabdominal claw. *(B–D and G–H) After Orlova-Bienkowskaja (2001).*

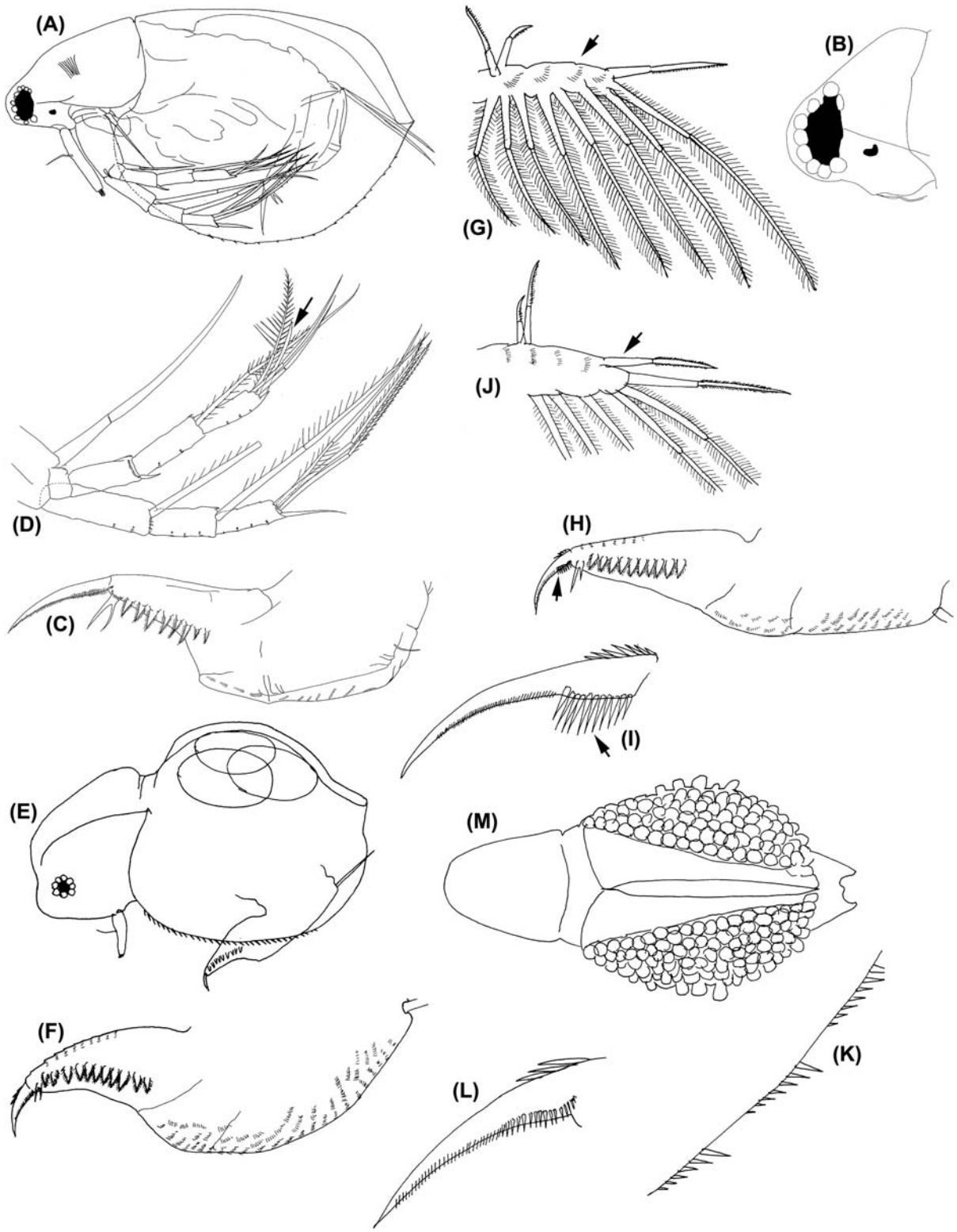


FIGURE 16.2.19 Representatives of Moinidae: (A–D) *Moinodaphnia macleayi*, general view, head, postandomen and antenna II; (E–G) *Moina salina*, general view, postabdomen and limb I; (H–J) *Moina brachiata*, postabdomen, postabdominal claw and limb I; (K–M) *Moina weismanni*, postero-ventral margin of valve, postabdominal claw in lateral view and ephippial female in dorsal view.

Branchiopoda: Anomopoda: Moinidae: Genera

1 Antenna II exopod (of four antennomeres) with apical spine very large (Figs. 16.2.19 A–D) ..... *Moinodaphnia macleayi* (King, 1853) [Japan, Korea, southern Asia]

1′ Antenna II exopod (of four antennomeres) with short apical spine ..... ***Moina*** **[p. 682]**

Branchiopoda: Anomopoda: Moinidae: *Moina*: Species

1 Thoracic limb I "penultimate segment" anterior face with a long seta 2

1′ Thoracic limb I "penultimate segment" anterior face without a seta (Figs. 16.2.19 E–G) ..... *Moina salina* Daday, 1888 species group [Europe to Mongolia, mainly in steppe saline water bodies]

2(1) Postabdominal claw with basal pecten large spines three times or less in length than distal pecten setule length 3

2′ Postabdominal claw with basal pecten large spines at least five times longer than distal pecten setule length (Figs. 16.2.19 H–J) .... *Moina brachiata* (Jurine, 1820) species group [Palaearctic]

3(2) Posterior valve margin setulae alternate in size 4

3′ Posterior valve margin setulae do not alternate in size 5

4(3) Head and valve dorsum with few setules; ephippium with strong prominences (Figs. 16.2.19 K–M) .... *Moina weismanni* Ishikawa, 1896 [southern Europe. Oriental region]

4′ Head and valve dorsum glaborus; ephippium with polygons (Figs. 16.2.20 A–E) ..... *Moina micrura* Kurz, 1874 species group [Palaearctic. Pantropical]

5(3) Limb I "penultimate segment" bearing rigid seta with relatively thin setules (Fig. 16.2.20 G) 6

5′ Limb I "penultimate segment" bearing rigid seta with strong denticles (Fig. 16.2.20 F) .... *Moina macrocopa* (Straus, 1820) species group [Palaearctic]

6(5) Valve ventral margin with long setae, remarkably longer than posterior valve margin setules (Figs. 16.2.20 G, H) .... *Moina lipini* Smirnov, 1976 [central Palaearctic]

6′ Ventral valve margin with relatively short setae, only somewhat longer than posterior valve margin setules (Fig. 16.2.20 I) ..... *Moina ephemeralis* Hudec, 1997 [central Europe]

Branchiopoda: Anomopoda: Ilyocryptidae: *Ilyocryptus*: Species

1 Molting complete 2

1′ Molting incomplete (carapace with longitudinal ridges) 6

2 Valves lacking lateral horns 3

2′ Valve with a lateral horn (Fig. 16.2.21 A) ..... *Ilyocryptus cornutus* Mordukhai-Boltovskoi & Chirkova, 1972 [northern Palaearctic]

3(2) Postabdomen with anus approximately midway along dorsal margin, preanal margin short 4

3′ Postabdomen with anus subdistal, preanal margin long 5

4(3) Small denticles near preanal teeth (Figs. 16.2.21 B–D) ..... *Ilyocryptus agilis* Kurz, 1874 [Palaearctic]

4′ Denticles absent near preanal teeth (Fig. 16.2.21 E) ..... *Ilyocryptus yooni* Jeong, Kotov & Lee, 2013 [Japan, Korea, Russia (China?)]

5(3) Posterior valve margin setae with inflated trunks, armed with fine setules and lacking spiniform setules; postabdomen preanal margin basal half with large spines present (Figs. 16.2.21 F, G) ..... *Ilyocryptus acutifrons* Sars, 1862 [Palaearctic]

5′ Posterior valve margin setae with trunks uniform, armed with several spiniform setules; postabdomen preanal margin basal half without spines (Figs. 16.2.21 H, I) ..... *Ilyocryptus uenoi* Kotov & Tanaka, 2004 [Japan]

6(1) Anus subdistal, preanal margin long 7

6′ Anus approximately in middle of dorsal margin of postabdomen, preanal margin short 8

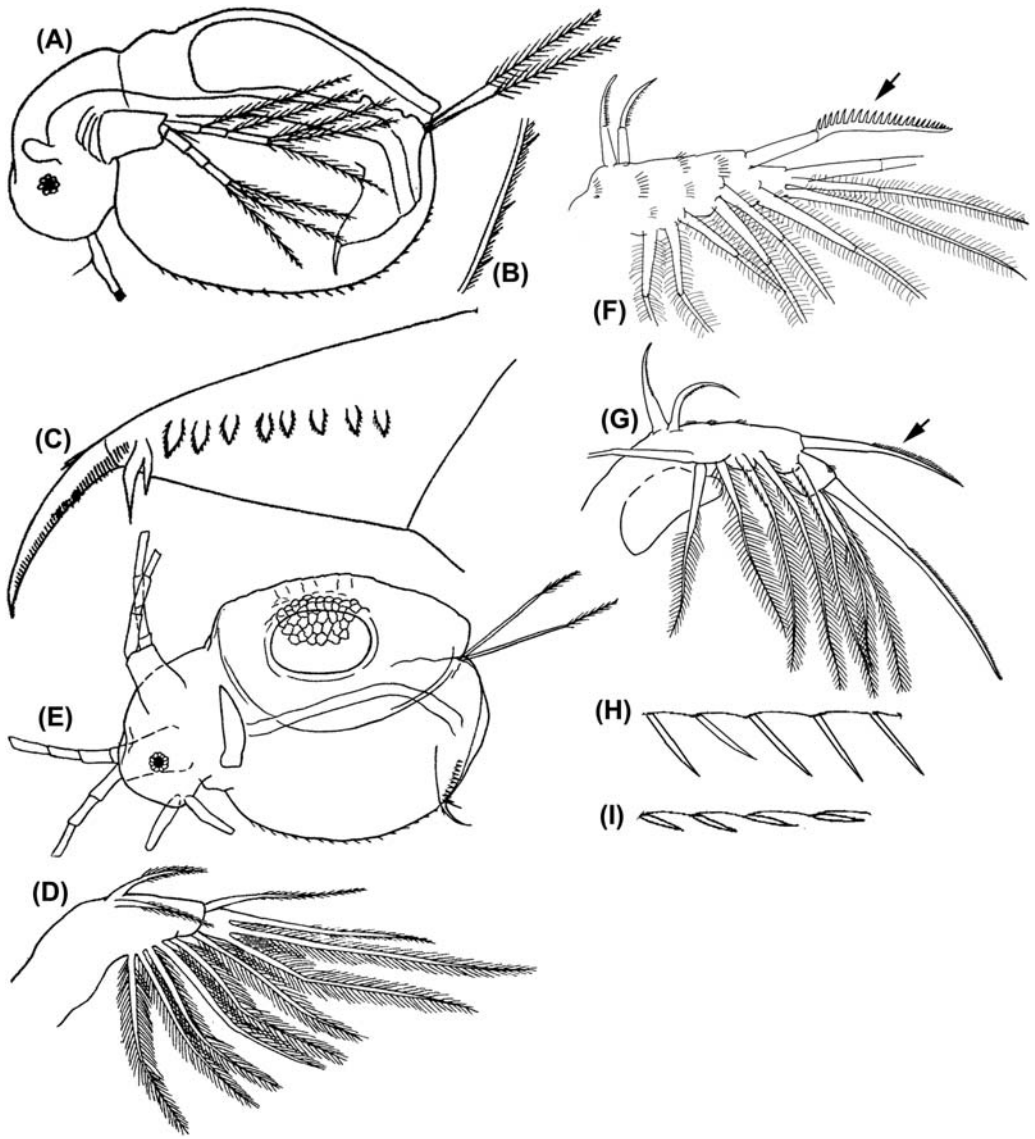


FIGURE 16.2.20 Representatives of *Moina* (Moinidae): (A–E) *Moina micrura*, general view of parthenogenetic female, postero-ventral portion of valve, postabdomen, limb I and general view of ephippial female; (F) *Moina macrocopa*, limb I; (G and H) *Moina lipini*, limb I and setae at valve posterior margin; (I), *Moina ephemeralis,* setae at valve posterior margin.

7(6)	Preanal teeth small and numerous (17–27) (Fig. 16.2.21 J) ..... *Ilyocryptus vitali* Chirkova, 1982 [Russia]	
7′	Preanal teeth relatively long and less numerous (16–19) (Fig. 16.2.21 K) ..... *Ilyocryptus spinosus* Štifter, 1988 [central and northern Europe]	
8(6)	Abdominal basalmost lateral seta located on preanal margin, or anal margin, or postanal margin immediately near anus	9
8′	Abdominal basalmost lateral seta located on postanal margin relatively far from anus (Figs. 16.2.22 A, B) .... *Ilyocryptus spinifer* Herrick, 1882 [Asian Palaearctic]	
9	At least some preanal teeth paired	10
9′	All preanal teeth singular	11
10(9)	Preanal margin long, with 9–12 teeth (Figs. 16.2.22 C, D) ..... *Ilyocryptus cuneatus* Štifter, 1988 [Palaearctic]	

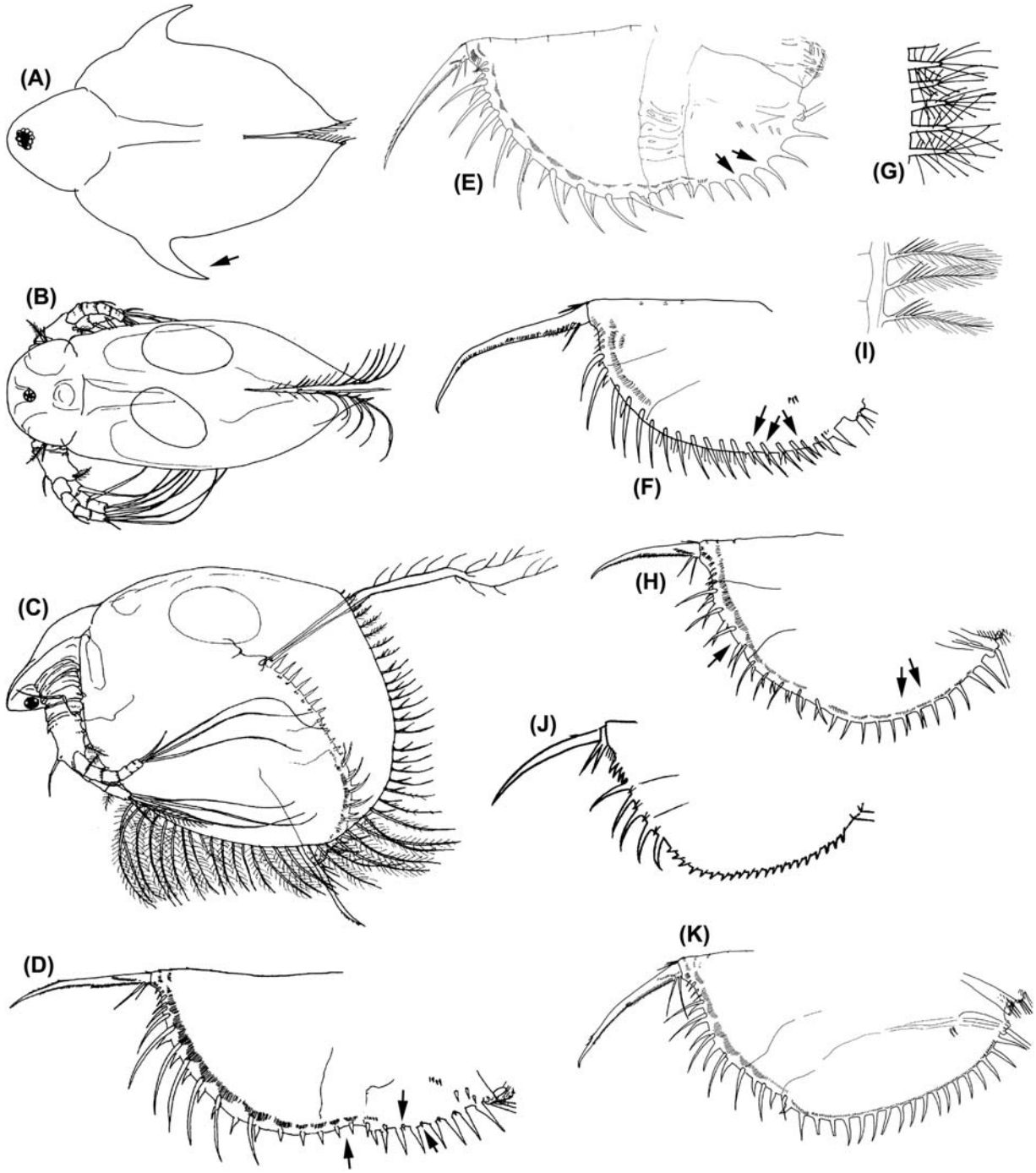


FIGURE 16.2.21 Representatives of Ilyocryptidae: (A) *Ilyocryptus cornutus*, dorsal view; (B–D) *Ilyocryptus agilis*, dorsal, lateral view and postabdomen; (E) *Ilyocryptus yooni,* postabdomen; (F and G) *Ilyocryptus acutifrons*, postabdomen and armature of posterior valve margin; (H and I) *Ilyocryptus uenoi*, postabdomen and armature of posterior valve margin; (J) *Ilyocryptus vitali*, postabdomen; (K) *Ilyocryptus spinosus*, postabdomen.

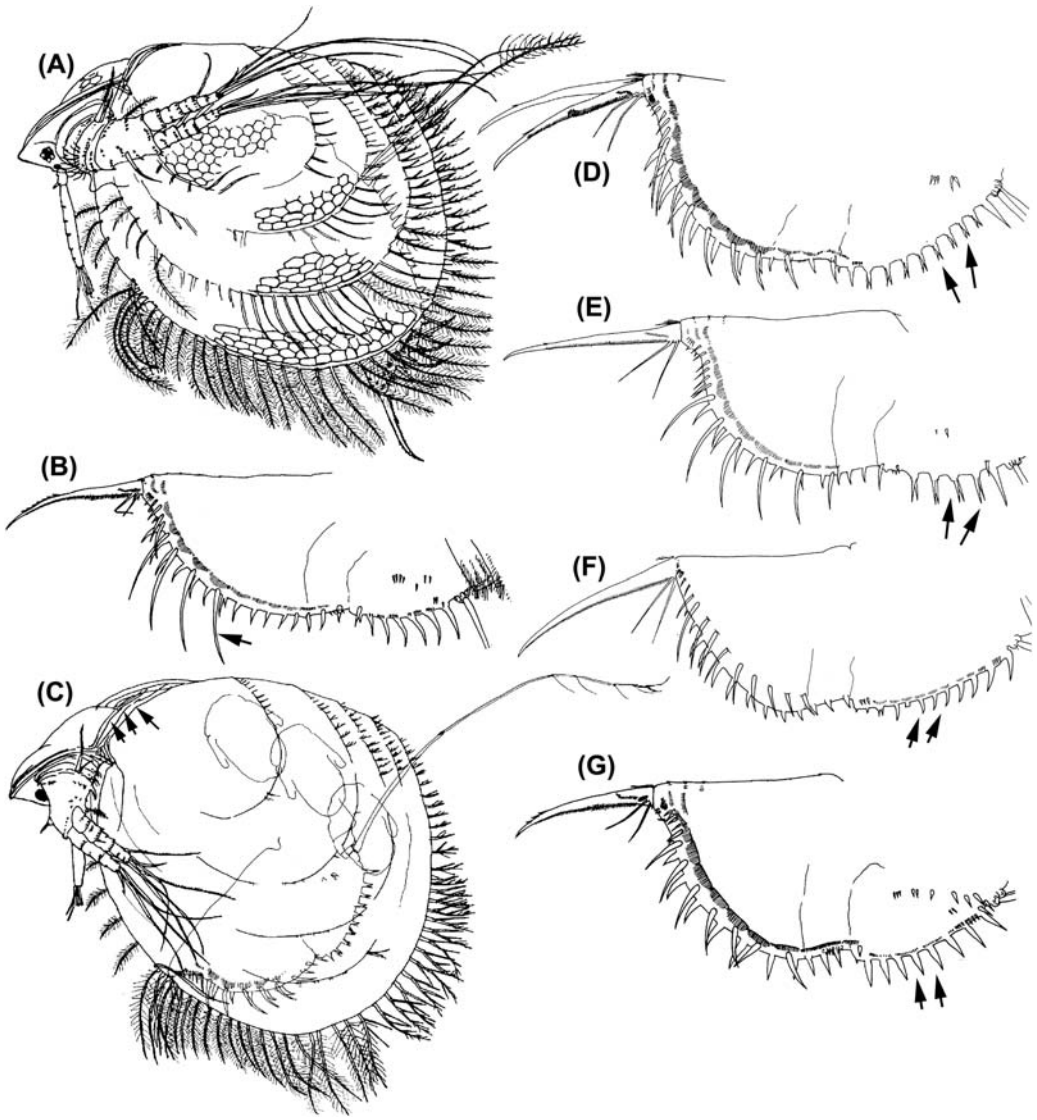


FIGURE 16.2.22 Representatives of Ilyocryptidae: (A and B) *Ilyocryptus spinifer*, lateral view and postabdomen; (C and D) *Ilyocryptus cuneatus*, lateral view and postabdomen; (E) *Ilyocryptus silvaeducensis*, postabdomen; (F) *Ilyocryptus sordidus*, postabdomen; (G) *Ilyocryptus sarsi*, postabdomen.

10′	Preanal margin short, with 5–8 teeth (Fig. 16.2.22 E)	*Ilyocryptus silvaeducensis* Romijn, 1919 [northwestern Europe]
11(9)	Females up to 1.0 mm; preanal teeth curved regularly and slightly backwards (Fig. 16.2.22 F)	*Ilyocryptus sordidus* (Liévin, 1848) (Holarctic, possible species group)
11′	Females up to 0.6 mm; preanal teeth straight (Fig. 16.2.22 G)	*Ilyocryptus sarsi* Stingelin, 1913 s.lat. [Asia, possible species group]

Branchiopoda: Anomopoda: Ophryoxidae: *Ophryoxus*: Species

1	Postabdomen relatively long, cuneiform; postanal teeth decreased in size proximally	2
1′	Postabdomen relatively short, its dorsodistal portion widely rounded, postanal teeth largest in middle of margin (Figs. 16.2.23 C, D)	*Ophryoxus zini* Smirnov, 1992 [Russia (Lake Bolon)]
2(1)	Prelabral outgrowth acute (Figs. 16.2.23 E–H)	*Ophryoxus gracilis* Sars, 1862 [northern Palaearctic]
2′	Prelabral outgrowth blunt (Figs. 16.2.23 I–K)	*Ophryoxus kolymensis* Smirnov, 1992 [northern Palaearctic]

Branchiopoda: Anomopoda: Macrothricidae: Genera

1	Intestine without convolutions	2
1′	Intestine with convolutions	5
2(1)	Carapace ventral margin setae not lanceolate and not flattened	3
2′	Carapace ventral margin setae lanceolate and flattened (Figs. 16.2.23 L, M) ... *Lathonura rectirostris* (O.F. Müller, 1785) [Palaearctic]	
3(2)	Body either moderately compressed or noncompressed laterally	4
3′	Body very strongly laterally compressed, with a very high and sharp dorsal keel (Fig. 16.2.23 N) ... *Bunops serricaudata* (Daday, 1888) [southern Palaearctic]	
4(3)	Limb IV exopodite with 2 or 3 setae ... ***Macrothrix* [p. 686]**	
4′	Limb IV exopodite with 5 setae (Figs. 16.2.23 O–Q) ... *Wlassiscia pannonica* Daday, 1904 [southern Palaearctic]	
5(1)	Antenna I with lateral margin serrate, lacking long setae; antenna II exopod (with four articles) with only three apical setae (Figs. 16.2.24 A–C) ... *Drepanothrix dentata* (Euren, 1861) [Palaearctic]	
5′	Antenna I with smooth lateral margin, bearing long setae; antenna II exopod (with four articles) with three apical and a lateral setae (Figs. 16.2.24 D–F) ... *Streblocerus serricaudatus* (Fischer, 1849) [Palaearctic]	

Branchiopoda: Anomopoda: Macrothricidae: *Macrothrix*: Species

1	Body without setae and strong lateral horns	2
1′	Body with numerous setae and strong paired lateral horns (Fig. 16.2.24 G) ... *Macrothrix pennigera* Shen, Sung & Chen, 1961 [China, Korea]	
2(1)	Anal flaps absent; head ventral margin straight or slightly convex	3
2′	Anal flaps present; head ventral margin with a strong projection (Fig. 16.2.24 H–J) ... *Macrothrix odiosa* Gurney, 1916 [southern Palaearctic]	
3(2)	Carapace dorsal margin smooth or with very small folds	4
3′	Carapace dorsal margin with a strong, serrated keel (Fig. 16.2.24 K) ... *Macrothrix laticornis* (Jurine, 1820) [Holarctic]	
4(3)	Female antenna I widening distally	5
4′	Female antenna I baciliform	7
5(4)	Carapace dorsal margin smooth or with minute folds	6
5′	Carapace dorsal margin with distinct folds, appearing like finely serrated (Figs. 16.2.25 A–C) ... *Macrothrix spinosa* King, 1853 [central and southern Asia, China, northern Africa. Pantropical]	
6(5)	Postabdominal claw short; aesthetascs strongly differ in size (Figs. 16.2.25 D–F) ... *Macrothrix hirsuticornis* Norman & Brady, 1867 [Holarctic, possible species group]	
6′	Postabdominal claw long; aesthetascs slightly differ in size (Figs. 16.2.25 G, H) ... *Macrothrix dadayi* Behning, 1941 [western and central Palaearctic]	
7(4)	Postabdomen basal portion with a projection, bearing postabdominal setae, *M. rosea* species group	8
7′	Postabdomen basal portion without a projection (Figs. 16.2.25 I, J) ... *Macrothrix tripectinata* Weisig, 1934 [Caucasus, Altai, and Pamirs mountains]	
8(7)	Postabdominal seta distal portion as long as several diameters of the seta; antenna II endopod, proximal article with seta without strong spinulae	9
8′	Postabdominal seta distal portion as long as two diameters of the seta; antenna II endopod, proximal article with seta bearing two or three strong spinulae (Figs. 16.2.25 K–M) ... *Macrothrix triserialis* Brady, 1886 [central and southern Asia, China, northern Africa. Pantropical]	
9(8)	Postabdomen proximal projection large; antenna II endopod, proximal article with seta bearing sparse spinulae (Figs. 16.2.25 N–Q) ... *Macrothrix rosea* (Liévin, 1848) [Holarctic]	
9′	Postabdomen proximal projection comparatively small; antenna II endopod, proximal article with seta bearing dense spinulae (Figs. 16.2.25 R, S) ... *Macrothrix tabrizensis* Dumont, Silva-Briano & Babu, 2002 [Iran, central Asia]	

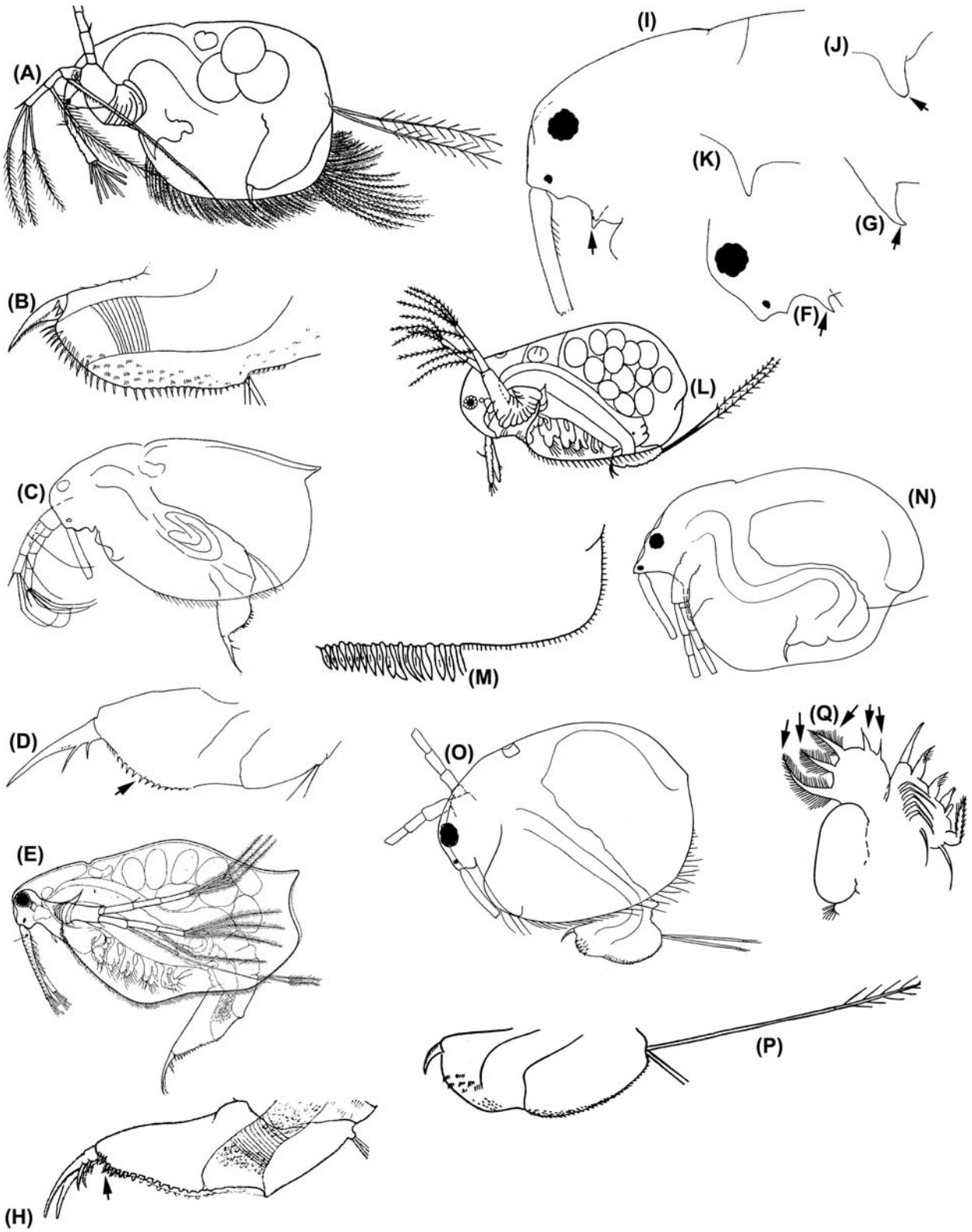


FIGURE 16.2.23 Representatives of Acantholeberidae (A and B), Ophryoxidae (C−K), and Macrothricidae (L−Q): (A and B) *Acantholeberis curvirostris*, lateral view and postabdomen; (C and D) *Ophryoxus zini,* lateral view and postabdomen; (E−H) *Ophryoxus gracili*s, lateral view, head, prelabral outgrowth, and postabdomen; (I−K) *Ophryoxus kolymensis*, head and prelabral outgrowths of two females; (L and M) *Lathonura rectirostris*, lateral view and posteroventral valve portion; (N) *Bunops serricaudata*; (O−Q) *Wlassiscia pannonica*, lateral view, postabdomen, and limb IV.

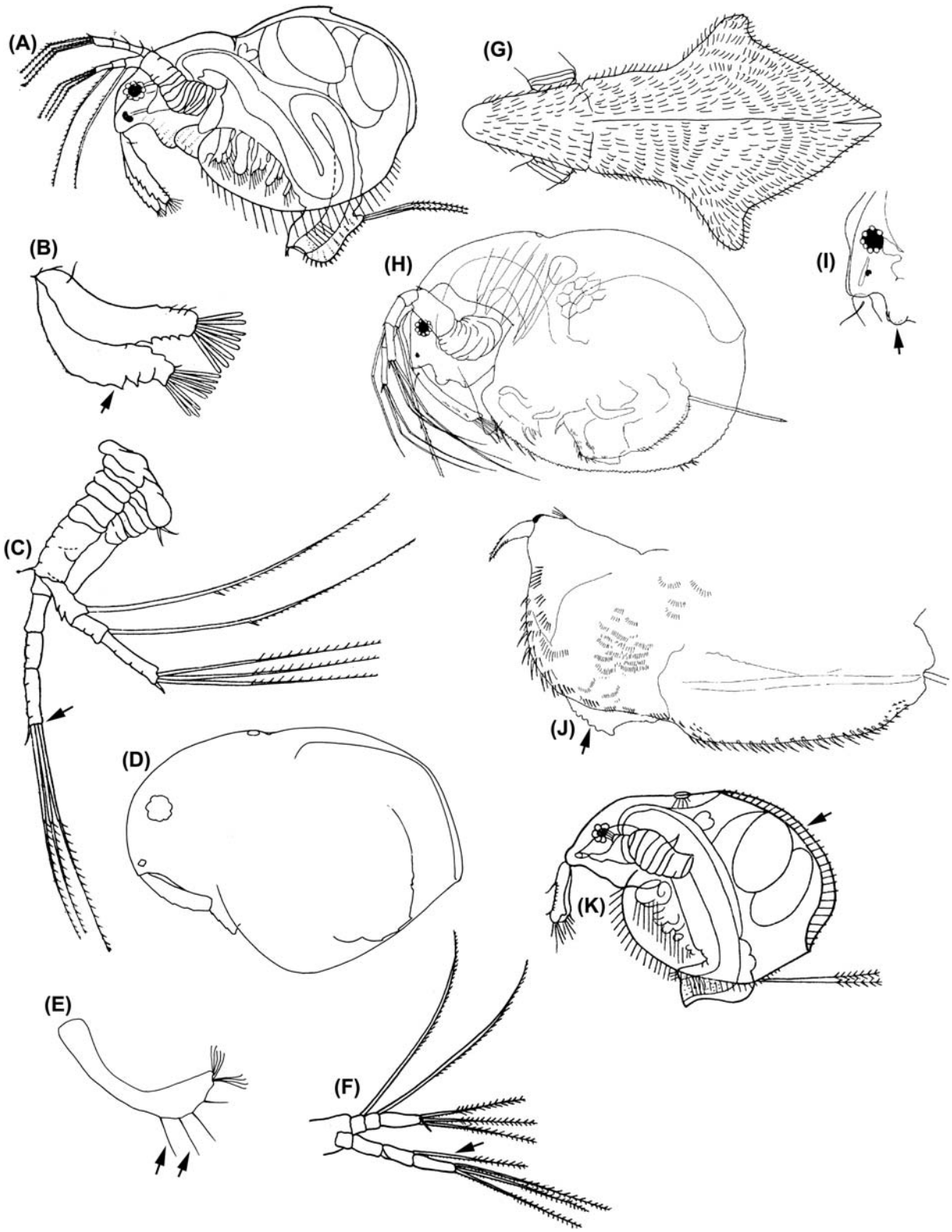


FIGURE 16.2.24 Representatives of Macrothricidae: (A–C) *Drepanothrix dentata*, general view, antennae I, antenna II; (D–F) *Streblocerus serricaudatus*, general view, antenna I, antenna II. (G) *Macrothrix pennigera*, dorsal view; (H–J) *Macrothrix odiosa,* general view, head and postabdomen; (K) *Macrothrix laticornis*. *(A–C and K) After Lilljeborg (1901).*

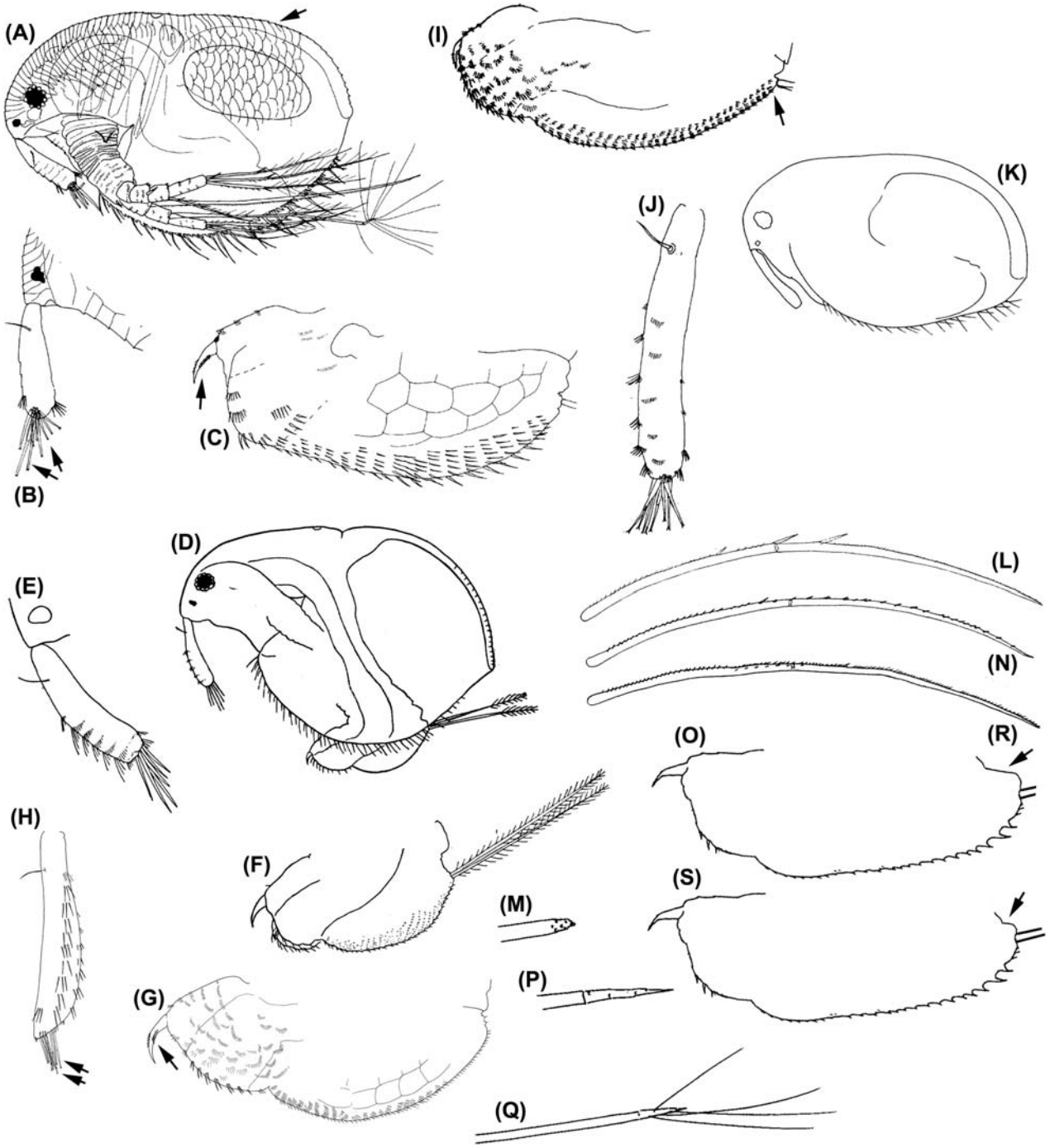


FIGURE 16.2.25 Representatives of *Macrothrix* (Macrothricidae): (A–C) *Macrothrix spinosa*, lateral view, head, and postabdomen; (D–F) *Macrothrix hirsuticornis*, lateral view, antenna I, and postabdomen; (G and H) *Macrothrix dadayi*, postabdomen and antenna I; (I and J), *Macrothrix tripectinata*, postabdomen and antenna I; (K–M) *Macrothrix triserialis*, general view, seta on proximal segment of antennal andopod, distal segment of postabdominal seta; (N–Q) *Macrothrix rosea*, seta at proximal segment of antennal endopod, postabdomen and distal segment of postabdominal seta; (R and S) *Macrothrix tabrizensis*, seta on proximal segment of antennal endopod and postabdomen.

Branchiopoda: Anomopoda: Bosminidae: Genera

1 Antennae I proximal portions not fused; antenna II exopod of four articles ..... ***Bosmina*** **[p. 690]**

1′ Antennae I proximal portions fused; antenna II exopod of three articles (Figs. 16.2.19 A, B)..... ..... *Bosminopsis deitersi* Richard, 1895 species complex
[Palaearctic. Oriental]

Branchiopoda: Anomopoda: Bosminidae: *Bosmina*: Subgenera

1 Lateral head pore situated near head shield lateral margin, close to antenna II 2

1′ Lateral head pore situated far from head shield lateral margin, closer to mandibular articulation than to antenna II .... ***Bosmina* (*Eubosmina*) [p. 690]**

2(1) Lateral head pore situated very close to head shield lateral margin; male postabdomen preanal margin with a deep depression (Figs. 16.2.26 C–F) ..... *Bosmina* (*Bosmina*) *longirostris* (O. F. Müller, 1785)
[cosmopolitan]

2′ Lateral head pore at a short distance from head shield lateral margin; male postabdomen preanal margin with a very shallow depression (Figs. 16.2.26 G–J) ..... *Bosmina* (*Sinobomina*) *fatalis* Burckhardt, 1924
[China, Japan, Korea, Russia. Possible species complex]

Branchiopoda: Anomopoda: Bosminidae: *Bosmina*: *Bosmina* (*Eubosmina*): Species

1 Postabdomen postanal portion massive, postanal depression smooth; claw base with two or three denticles (Figs. 16.2.26 K, L) .... *Bosmina* (*Eubosmina*) *tanakai* Kotov, Ishida, & Taylor, 2009
[Russia. Japan]

1′ Postabdomen postanal portion relatively slender, making a distinct obtuse angle with anal margin; claw base with more than five denticles (Figs. 16.2.26 M–P) ..... *Bosmina* (*Eubosmina*) *coregoni* Baird, 1857 species group
[Palaearctic]

Branchiopoda: Anomopoda: Eurycercidae: *Eurycercus*: Species

1 Dorsal head pores on flat head shield (no hemispherical projection or transverse fold in this portion); major head pore ring not elevated or slightly elevated above head shield surface; antenna I elongated prominently; intestine with a double loop (Fig. 16.2.27 A) 2

1′ Dorsal head pores on a hemispherical projection or on a transverse fold in head shield posterior portion with a posterior indentation, or on hemispherical projection located on a transverse fold, but never on a flat head shield surface; antenna I moderately elongated; intestine with a single loop 3

2(1) Major head pore ring not projecting above head shield surface, no cuticular prominence in pore center (Fig. 16.2.27 A, B) .... *Eurycercus* (*Teretifrons*) *glacialis* Lilljeborg, 1887
[Northern Palaearctic]

2′ Major head pore ring projecting above head shield, major head pore surface with a low projection in middle (Fig. 16.2.27 C) ....*Eurycercus* (*Teretifrons*) *chernovi* Bekker & Kotov, 2016
[Arctic Russia: Taimyr Peninsula]

3(1) Parthenogenetic female dorsum without medial keel; head pores on a hemispherical projection 4

3′ Parthenogenetic female dorsum with a medial keel; head pores on a transverse fold (Fig. 16.2.27 D–F) .... *Eurycercus* (*Eurycercus*) *lamellatus* (O. F. Müller, 1776)
[Palaearctic]

4(3) Median labral keel large, subequal in length to antenna I 5

4′ Median labral keel short, approximately half as long as antenna I (Fig. 16.2.27 G, H) .... *Eurycercus* (*Eurycercus*) *pompholygodes* Frey, 1975
[Arctic and Subarctic]

5(4) Medial labral keel apex angular; limb I, distal lobe medial hamulate seta of moderate size (Fig. 16.2.27 I–L) ....*Eurycercus* (*Eurycercus*) *nipponica* Tanaka & Fujita, 2002
[Japan, Far East of Russia]

5′ Medial labral keel apex rounded; limb I, distal lobe medial hamulate seta of very large (Fig. 16.2.27 M–P) ....*Eurycercus* (*Eurycercus*) *macracanthus* Frey, 1973
[China, Russia]

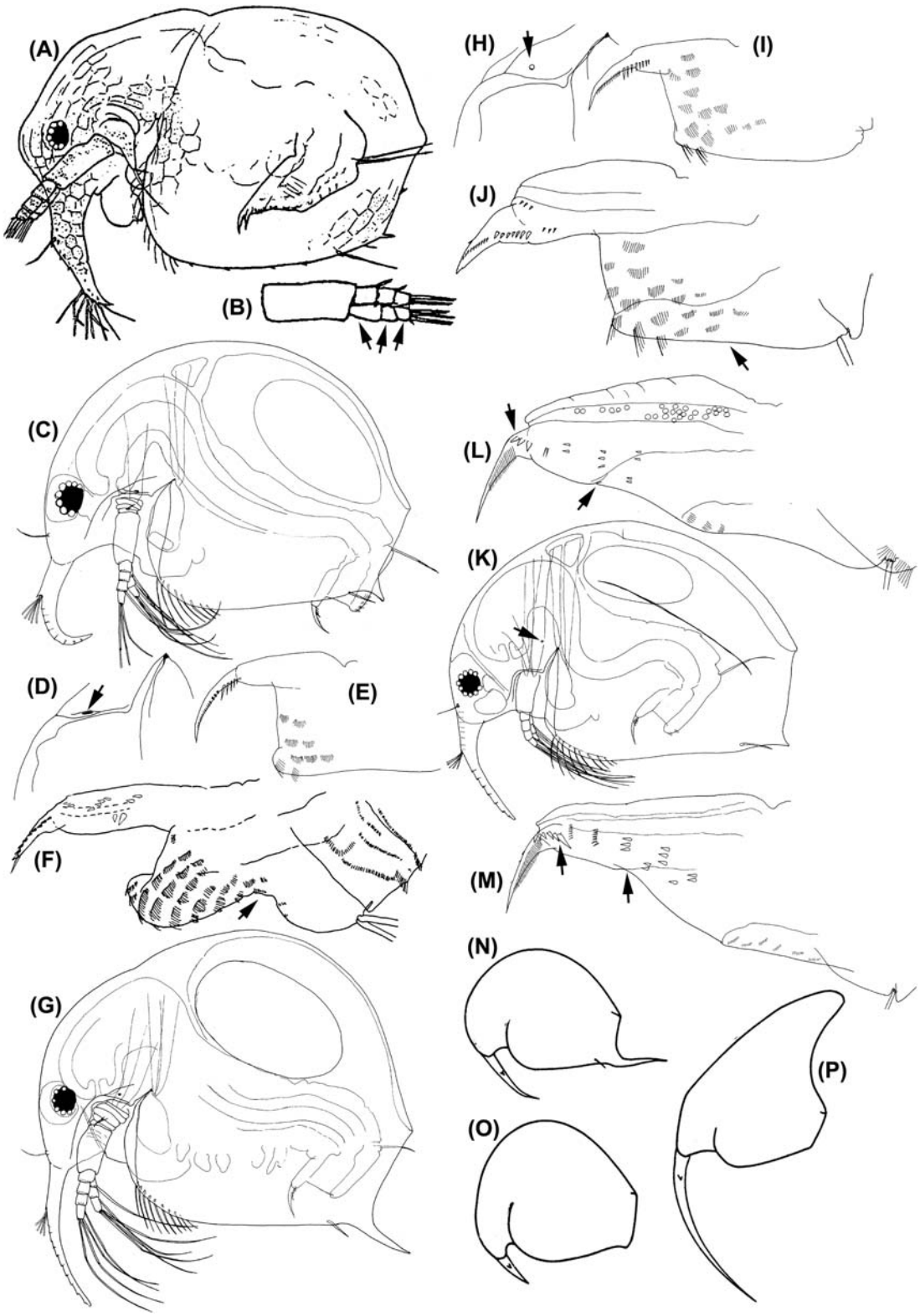


FIGURE 16.2.26 Representatives of Bosminidae: (A and B), *Bosminopsis deitersi*, general view and antenna II; (C–F) *Bosmina* (*Bosmina*) *longirostris*, general view, lateral head pore, postabdomen of female and male; (G–J) *Bosmina* (*Sinobomina*) *fatalis*, general view, lateral head pore, postabdomen of male and female; (K and L) *Bosmina* (*Eubosmina*) *tanakai*, general view of female and postabdomen of male; (M–P) *Bosmina* (*Eubosmina*) *coregoni* species group, postabdomen of male and different morphotypes of females.

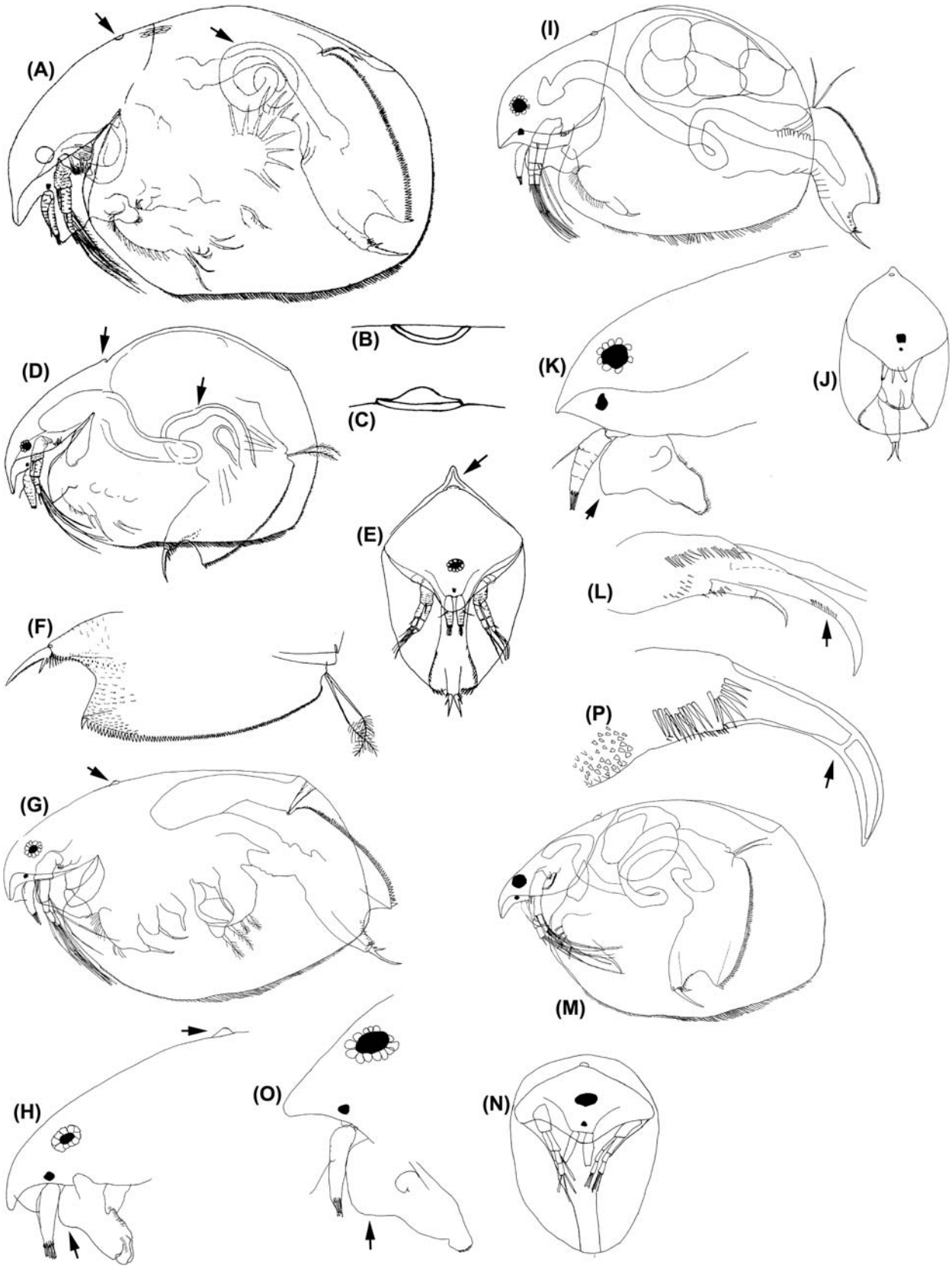


FIGURE 16.2.27 Representatives of Eurycercidae: (A and B) *Eurycercus* (*Teretifrons*) *glacialis*, general view and head pore; (C) *Eurycercus* (*Teretifrons*) *chernovi,* head pore; (D–F) *Eurycercus* (*Eurycercus*) *lamellatus*, lateral, anterior view and postabdomen of parthenogenetic female; (G and H) *Eurycercus* (*Eurycercus*) *pompholygodes*, general view and head; (I–L), *Eurycercus* (*Eurycercus*) *nipponica*, lateral, anterior view, head and distal portion of limb I of parthenogenetic female; (M–P), *Eurycercus* (*Eurycercus*) *macracanthus*, general, anterior view, head and largest seta of limb I of parthenogenetic female.

Branchiopoda: Anomopoda: Chydoridae: Subfamilies

1 Thoracic limb IV, exopodite with six setae ..... **Aloninae [p. 693]**

1′ Thoracic limb IV, exopodite with seven setae ..... **Chydorinae [p. 710]**

Branchiopoda: Anomopoda: Chydoridae: Aloninae: Genera

1 Postabdomen length ≥3.5x maximum height 2

1′ Postabdomen length <3.5x maximum height 8

2(1) Postabdomen claw base with cluster of long setae 3

2′ Postabdomen claw base without cluster of long setae 4

3(2) Head and valves with an obvious dorsal keel; postabdomen marginal denticles very small and grouped ..... ***Acroperus* [p. 696]**

3′ Head and valves without a dorsal keel; postabdomen marginal denticles large and single (Figs. 16.2.28 A, B) ..... *Alonopsis elongatus* Sars, 1862
[Northern and central Palaearctic]

4(2) Head and valves without a dorsal keel 5

4′ Head and valves with an obvious dorsal keel ..... ***Camptocercus* [p. 696]**

5(4) Rostrum short and broad 6

5′ Rostrum long and narrow ..... ***Kurzia* [p. 696]**

6(5) Postabdomen not curved, its ventral and postanal margins straight 7

6′ Postabdomen curved, with convex ventral and strongly concave postanal margin ..... ***Kozhowia* [p. 696]**

7(6) Postabdomen marginal denticles small, grouped, similar to lateral groups of setae (Figs. 16.2.28 C, D) ..... *Tretocephala ambigua* (Lilljeborg, 1901)
[Europe, Siberia]

7′ Postabdomen marginal denticles large, single, distalmost denticle(s) much larger than others (Figs. 16.2.28 E, F) ..... *Oxyurella tenuicaudis* (Sars, 1862)
[Palaearctic]

8(1) At least ocellus present 9

8′ Both eye and ocellus absent ..... ***Brancelia* [p. 697]**

9(8) Body compressed laterally, valves from previous molts not retained 10

9′ Body sphaerical, valves from previous molts retained ..... ***Monospilus* [p. 697]**

10(9) Head shield anterior margin not broadly rounded, rostrum present 11

10′ Head shield anterior margin broadly rounded, expanding anteriorly (Figs. 16.2.28 G, H) ..... *Graptoleberis testudinaria* (Fisher, 1851) species group
[Palaearctic]

11(10) Rostrum long, curved 12

11′ Rostrum short, broad 13

12(11) Postabdomen distal teeth large, single (Figs. 16.2.28 I, J) ..... *Rhynchotalona falcata* Sars, 1862
[Europe, Siberia, Mongolia]

12′ Postabdomen distal teeth small and grouped (Figs. 16.2.29 A, B) ..... *Nedorhynchotalona chiangi* Kotov & Sinev, 2011
[China, Korea, Russia]

13(11) Animal ovoid in lateral view, with ventral carapace margin weakly convex to straight; rostrum not truncated 14

13′ Animal rounded in lateral view, with ventral carapace margin strongly convex; rostrum truncated ..... ***Leberis* [p. 697]**

14(13) Postabdomen with small lateral setae, longest setae less than twice the width of postabdominal claw base 15

14′ Postabdomen with very long and thick lateral setae, longest setae length equal to three or more times the width of postabdominal claw base ..... ***Leydigia* [p. 697]**

15(14) Lateral head pores without cavities 16

15′ Lateral head pores with bilobed or trilobed cavities (cosmaria) below ..... ***Anthalona* [p. 698]**

16(15) Labral plate not cuneoform; antenna II exopod proximal article with spine well developed 17

16′ Labral plate narrow, cuneoform; antenna II exopod proximal article with spine very small, less than half length of middle article ..... ***Phreatalona* [p. 698]**

17(16) Valves with posterioventral angle without denticles, or, rarely, with 1−3 denticles, separated by about the width of denticle base or less 18

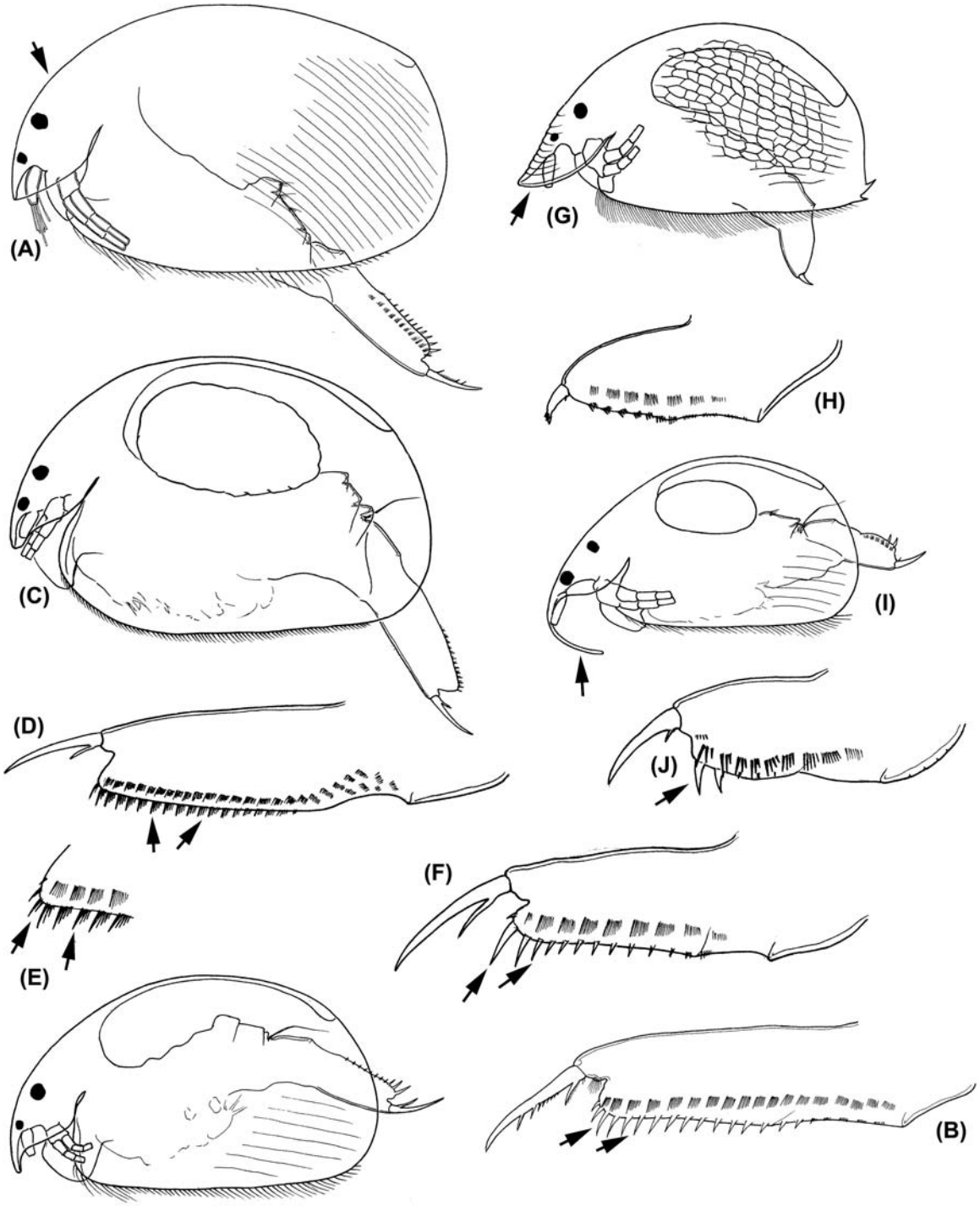


FIGURE 16.2.28 Representatives of Aloninae (Chydoridae): (A and B) *Alonopsis elongatus*, general view and postabdomen; (C and D) *Tretocephala ambigua*, general view and postabdomen; (E and F) *Oxyurella tenuicaudis*, general view and postabdomen; (G and H) *Graptoleberis testudinaria*, general view and postabdomen; (I and J) *Rhynchotalona falcata*, general view and postabdomen.

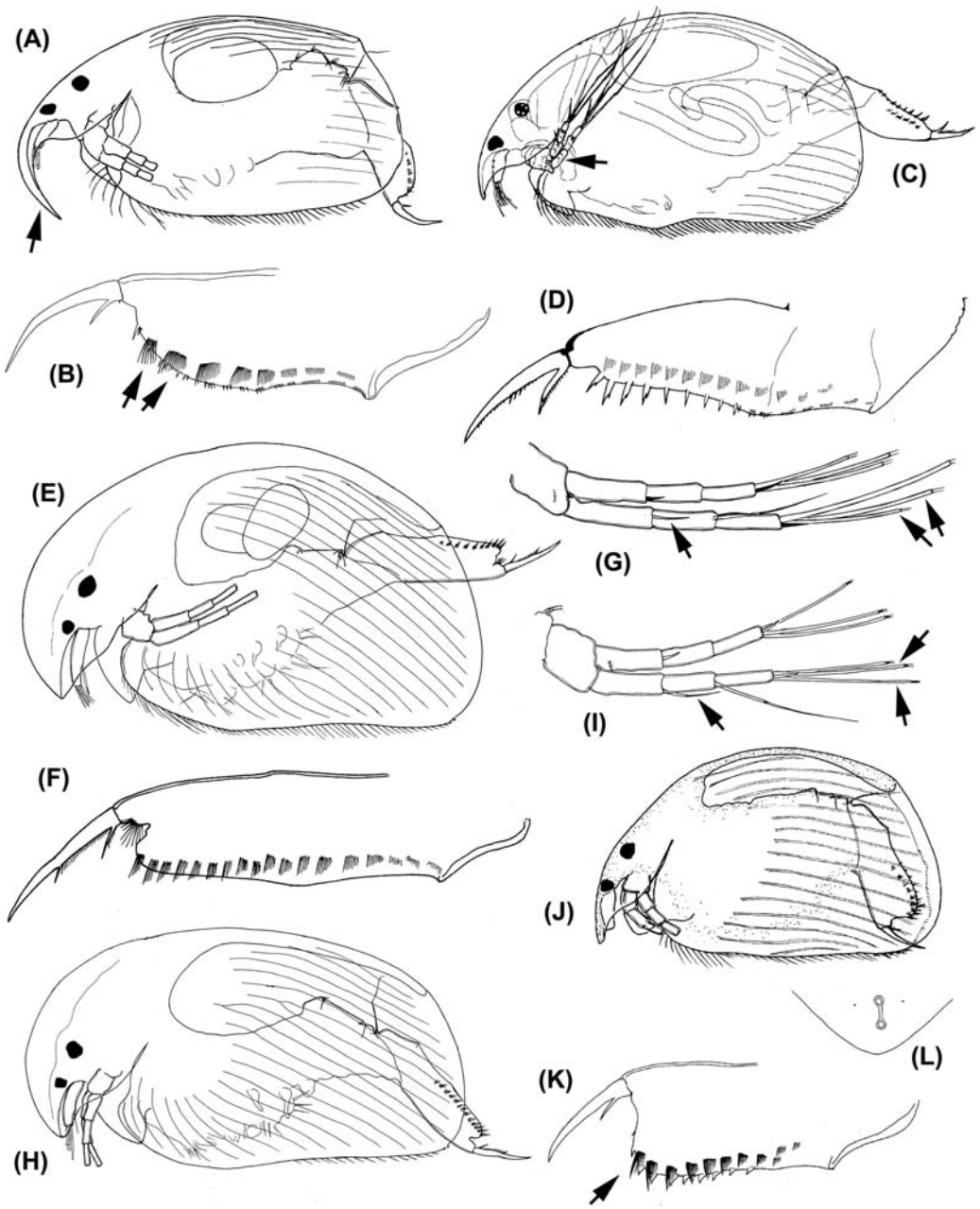


FIGURE 16.2.29 Representatives of Aloninae (Chydoridae): (A and B) *Nedorhynchotalona chiangi*, general view and postabdomen; (C and D) *Parakozhowia baikalensis*, general view and postabdomen; (E–G) *Acroperus harpae*, general view, postabdomen, and antenna II; (H and I) *Acroperus angustratus*, general view and antenna II; (J–L) *Alona intermedia*, general view, postabdomen, and head pores.

17′	Valves with posterioventral angle with 3−5 denticles, separated by at least twice the width of denticle base ..... ***Karualona*** **[p. 698]**
18(17)	Antenna II endopod, proximal article with seta present 19
18′	Antenna II endopod, proximal article with seta absent (Figs. 16.2.29 C, D) ..... *Parakozhowia baikalensis* (Vasiljeva & Smirnov, 1969) [Lake Baikal]

19(18)	Lateral head pores circular	20
19′	Lateral head pores slit shaped with pocket-like cavities below	***Flavalona*** **[p. 698]**
20(19)	Limb III exopodite with seven setae	21
20′	Limb III exopodite with six setae	***Coronatella*** *s. lato* (including *Alona elegans* group) **[p. 698]**
21(20)	Central and posterior main head pores at least with connection absent, or postabdomen basal spine very small	***Ovalona*** **[p. 699]**
21′	All main head pores connected; postabdomen basal spine well-developed	***Alona*** *s. lato* (excluding *elegans* group) **[p. 699]**

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Acroperus*: Species

1	Antenna II endopod significantly longer than exopod; endopod proximal article with seta much shorter than middle article; endopod distal article with setae different thickness (Figs. 16.2.29 E–G)	*Acroperus harpae* (Baird, 1834) [Palaearctic]
1′	Antenna II endopod and exopod of the same length; endopod proximal article with seta approximately as long as middle article; endopod distal article with setae of equal thickness (Figs. 16.2.29 H–I)	*Acroperus angustatus* Sars, 1862 [Palaearctic]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Camptocercus*: Species

1	Postabdominal claw basal spine not lanceolate, with maximum width in its base or middle	2
1′	Postabdominal claw basal spine lanceolate, with maximum width in its distal portion (Figs. 16.2.33 B)	*Camptocercus fennicus* Stenroos, 1898 [Europe, Siberia]
2(1)	Rostrum acute	3
2′	Rostrum truncate (Fig. 16.2.33 C)	*Camptocercus lilljeborgi* Schoedler, 1892 [Europe, Siberia]
3(2)	Valve posterioventral angle with denticles	4
3′	Valve posterioventral angle without denticles	5
4(3)	Valve posterioventral angle denticles dense and with a broad base; postabdomen distalmost marginal denticle size similar to preceeding denticles (Figs. 16.2.33 D–G)	*Camptocercus rectirostris* Sars, 1862 [Palaearctic]
4′	Valve posterioventral angle denticles sparse and with narrow bases; postabdomen distalmost marginal denticle size significantly larger than preceeding denticles (Figs. 16.2.33 H–J)	*Camptocercus streletskayae* Smirnov, 1998 [Siberia]
5(3)	Postabdomen marginal denticles triangular, narrow; body length not exceeding 0.65 mm (Figs. 16.2.33 K, L)	*Camptocercus vietnamensis* Thanh, 1980 [South Korea]
5′	Postabdomen marginal denticles broad, with margin serrated; body length up to 0.95 mm (Figs. 16.2.33 M–O)	*Camptocercus uncinatus* Smirnov, 1971 [China, Iraq, Korea, Mongolia, Romania, Siberia]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Kurzia*: Species

1	Rostrum and antenna I subequal in length (Figs. 16.2.36 L, M)	*Kurzia latissima* (Kurz, 1875) [Palaearctic]
1′	Rostrum 1.5–2 times longer than antenna I (Figs. 16.2.37 N–O)	*Kurzia longirostris* (Daday, 1898) [China, Korea]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Kozhowia*: Species

1	Postabdominal claw basal spine adpressed	2
1′	Postabdominal claw basal spine not adpressed, diverging from the claw	3
2(1)	Postanal marginal denticles single; postabdominal claw basal spine long, about half claw length (Figs. 16.2.36 A–C)	*Kozhowia gajewskajae* Vasiljeva & Smirnov, 1969 [Lake Baikal]

2′ Postanal marginal denticles clustered; postabdominal claw basal spine short, about one fourth claw length (Figs. 16.2.36 D–F) ..... *Kozhowia brevidentata* Vasiljeva & Smirnov, 1971 [Lake Baikal]

3(1) Postanal marginal denticles single (Figs. 16.2.36 G–I) ..... *Kozhowia primigenia* Vasiljeva & Smirnov, 1969 [Lake Baikal]

3′ Postanal marginal denticles in clusters (Figs. 16.2.36 J, K) ..... *Kozhowia kozhowi* Vasiljeva & Smirnov, 1969 [Lake Baikal]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Brancelia*: Species

These species are found in caves.

1 Postabdomen preanal margin long, slightly shorter than its distal (anal+postanal) portion..... 2

1′ Postabdomen preanal margin of moderate length, 1.5 times shorter than its distal (anal + postanal) portion (Fig. 16.2.32 A) ..... *Brancelia sketi* (Brancelj, 1992) [Slovenia]

2(1) Postabdomen claw basal spine long, about half claw length (Fig. 16.2.32 B) ..... *Brancelia stochi* (Brancelj, 1997) [Slovenia]

2′ Postabdomen claw basal spine shorter, about one third claw length (Figs. 16.2.32 D) ..... *Brancelia hercegovinae* (Brancelj, 1990) [Bosnia & Herzegovina]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Monospilus*: Species

1 Valves without lateral projections (Figs. 16.2.38 A, B) ..... *Monospilus dispar* Sars, 1862 [Palaearctic]

1′ Valves with lateral projections (Figs. 16.2.38 C–E) ..... *Monospilus daedalus* Kotov & Sinev, 2011 [Russia, South Korea]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Leberis* species

1 Limb I mediodistal lobe setae 2–3 with thin setulae of similar thickness (Figs. 16.2.37 I–L) ..... *Leberis diaphanus* (King, 1853) [South Korea, China]

1′ Limb I mediodistal lobe setae 2–3 basalmost elements thick spines, thicker and longer than other setulae (Fig. 16.2.37 M) ..... *Leberis punctatus* (Daday, 1898) [Mediterranean region]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Leydigia*: Species

1 Postabdominal claw with a strong basal spine 2

1′ Postabdominal claw with basal spine rudimentary or absent 3

2(1) Postabdomen with 6–7 distal groups of long setae; limb III exopodite with seven setae (Figs. 16.2.37 A, B) ..... *Leydigia korovchinskyi* Kotov & Alonso, 2010 [Spain]

2′ Postabdomen with 10–12 distal groups of long setae; limb III exopodite with five setae (Figs. 16.2.37 C–F) ..... *Leydigia leydigi* (Schödler, 1863) [Palaearctic]

3(1) Postabdomen distal groups of lateral setae with distalmost setule twice as long as preceeding one; limb III exopodite with three setae (Figs. 16.2.37 G–I) ..... *Leydigia acanthocercoides* (Fisher, 1854) [Palaearctic]

3′ Postabdomen distal groups of lateral setae with distalmost setule only slightly longer than preceeding one; limb III exopodite with five setae (Fig. 16.2.37 J) ..... *Leydigia iberica* Kotov & Alonso, 2010 [Spain]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Anthalona*: Species

1 Labral keel anterior margin with a single dorsal denticle (Figs. 16.2.31 I–L) ..... *Anthalona harti* Van Damme, Sinev & Dumont, 2011 [Subtropical Palaearctic]

1′ Labral keel anterior margin with group of dorsal setae (Fig. 16.2.31 M) ..... *Anthalona mediterranea* (Yalim, 2005) [Socotra Island, Turkey, United Arab Emirates]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Phreatalona*: Species

1 Eye and ocellus well developed, black; eye diameter subequal to width of antenna I 2

1′ Eye reduced, with diameter of half width of antenna I or absent 3

2(1) Valve posterioventral angle of with 1–3 denticles (Figs. 16.2.39 F, G) ..... *Phreatalona protzi* Hartwig, 1900 [Central Europe]

2′ Valve posterioventral angle without denticles (Figs. 16.2.39 H, I) ..... *Phreatalona labrosa* (Vasiljeva & Smirnov, 1969) [Lake Baikal]

3(1) Antenna II exopod with apical spine longer or equal to apical article; postabdomen lateral fascicle setae divergent distally, not parallel (Figs. 16.2.39 J–L) subterranean ..... *Phreatalona phreatica* Dumont, 1983 [France, Spain]

3′ Antenna II exopod with apical spine significantly shorter than apical article; postabdomen lateral fascicle setae parallel (Fig. 16.2.39 M) ..... *Phreatalona smirnovi* Petkovski & Flössner, 1972 [Lake Ohrid]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Karualona*: Species

1 Postanal margin about as long as anal margin (Figs. 16.2.35 J–L) ..... *Karualona iberica* (Alonso & Pretus, 1989) [Mediterranean, possibly central Asia]

1′ Postanal margin 1.5 to 2 times longer than anal margin (Figs. 16.2.35 M) ..... *Karualona karua* (King, 1853) *s. lato* [Subtropical Asia]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Flavalona*: Species

1 Lateral head pores as long slits, with length exceeding half distance between anterior and posterior main head pores 2

1′ Lateral head pores as short slits, with length about a third distance between anterior and posterior main head pores (Figs. 16.2.35 D–F) ..... *Flavalona rustica* (Scott, 1900) [Palaearctic]

2(1) Postabdomen distal dorsal angle acute, prominent (Figs. 16.2.35 A–C) ..... *Flavalona costata* (Sars, 1862) [Widely distributed in Palaearctic]

2′ Postabdomen distal dorsal angle obtuse, not prominent (Figs. 16.2.35 G–I) ..... *Flavalona weltneri* (Keilhack, 1905) [Central Europe]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Coronatella s. lato*: Species (including *Alona elegans* group)

1 Limb I, medial distal lobe, setae 2–3 with proximal setules 2

1′ Limb I, medial distal lobe, setae 2–3 with proximal spines (Figs. 16.2.32 E–H) ..... *Coronatella rectangula* (Sars, 1862) [Palaearctic]

2(1) Antenna II exopod proximal article with a seta 3

2′ Antenna II exopod proximal article without a seta (Figs. 16.2.32 I–L) ..... *Coronatella trachistriata* (Chen, 1993) [China, Russia]

3(2) Postabdomen with single row of lateral fasciae of setae 4

3′ Postabdomen with two similar size rows of lateral fasciae of setae (Figs. 16.2.34 A) ..... *Alona orellanai* Alonso, 1996 [Spain]

4(3) Valve posterioventral angle with more than 50 setae protruding beyond valve margin 5

4′ Valve posterioventral angle with less than 20 setae protruding beyond the valve margin (Figs. 16.2.32 M–O) ..... *Coronatella anemae* Van Damme & Dumont, 2008 [Central Asia]

5(4) Postabdomen preanal margin subequal to or longer than anal margin 6

5′ Postabdomen preanal margin shorter than anal margin (Figs. 16.2.34 B, C) ..... *Alona elegans* Kurz, 1875 [Central and western Europe]

6(5) Postabdomen postanal lateral fasciae each with distal seta as thick as others 7

6′ Postabdomen postanal lateral fasciae each with distal seta much thicker than others ((Figs. 16.2.34 D, E)) ..... *Alona salina* Alonso, 1996 [Spain]

7(6) Postabdomen distal marginal denticles single, as long as distal fascicle setae; postabdomen postanal portion 1.2 times longer than anal (Figs. 16.2.34 F, G) ..... *Alona irinae* Sinev, Alonso & Sheveleva, 2009 [Russia]

7′ Postabdomen distal marginal denticles in groups, two times shorter than distal fascicle setae; postabdomen postanal portion 1.5 times longer than anal (Figs. 16.2.34 H, I) ..... *Alona floessneri* Sinev, Alonso & Sheveleva, 2009 [Mongolia, Russia]

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Ovalona*: Species

1 Postabdominal claw basal spine well-developed 2

1′ Postabdominal claw basal spine very small (Figs. 16.2.38 F, G) ..... *Ovalona karelica* (Stenroos, 1897) [North and central Europe]

2(1) Major head pores with interconnections absent 3

2′ Major head pores with interconnections present between anterior and middle pore 4

3(2) Postabdomen narrowing distally; lateral head pores small round cavities (Figs. 16.2.38 H–J) .... *Ovalona nuragica* (Margaritora, 1971) [West Mediterranean]

3′ Postabdomen with parallel margins; lateral head pores small dots (Figs. 16.2.38 K–M) .... *Ovalona cambouei* Guerne & Richard, 1893 [Subtropical Palearctic]

4(2) Head shield distal portion acute; distance between middle and posterior major head pores increases with age, varies from 1.3 to 2–2.5 times the distance between middle and posterior pore (Figs. 16.2.39 A–C) ..... *Ovalona azorica* Frenzel & Alonso, 1988 [West portion of Iberian Peninsula, the Azores]

4′ Head shield distal portion round or blunt; distance between middle and posterior major head pores does not increase with age of specimens, about 0.8–1.2 times distance between middle and posterior pore (Figs. 16.2.39 D, E) ..... *Ovalona anastasia* Sinev, Alonso, Miracle & Sahuquillo, 2012 [West Mediterranean)

Branchiopoda: Anomopoda: Chydoridae: Aloninae: *Alona s. lato*: Species (excluding *Elegans* Group)

1 Two major head pores 2

1′ Three major head pores 3

2(1) Postabdomen widening distally; body size does not exceed 0.45 mm; limb I medial distal lobe without an unguiform seta (Figs. 16.2.29 J–L) ..... *Alona intermedia* Sars, 1862 [Palaearctic]

2′ Postabdomen with parallel margins; body size up to 1.1 mm; limb I medial distal lobe with a large unguiform seta (Figs. 16.2.30 A–D) ..... *Alona affinis* (Leydig, 1860) [Palaearctic]

3(1) Middle abdominal segment not covered by densely situated setules 4

3′ Middle abdominal segment covered by densely situated setules (Figs. 16.2.31 A, B) ..... *Alona setosocaudata* Vasiljeva et Smirnov, 1969 [Lake Baikal]

4(3) Postabdomen lateral group distal setules longer and thicker than others; limb I medial distal lobe with seta one well-developed, about third length of other two setae; limb I anterior margin with large single setules, not grouped 5

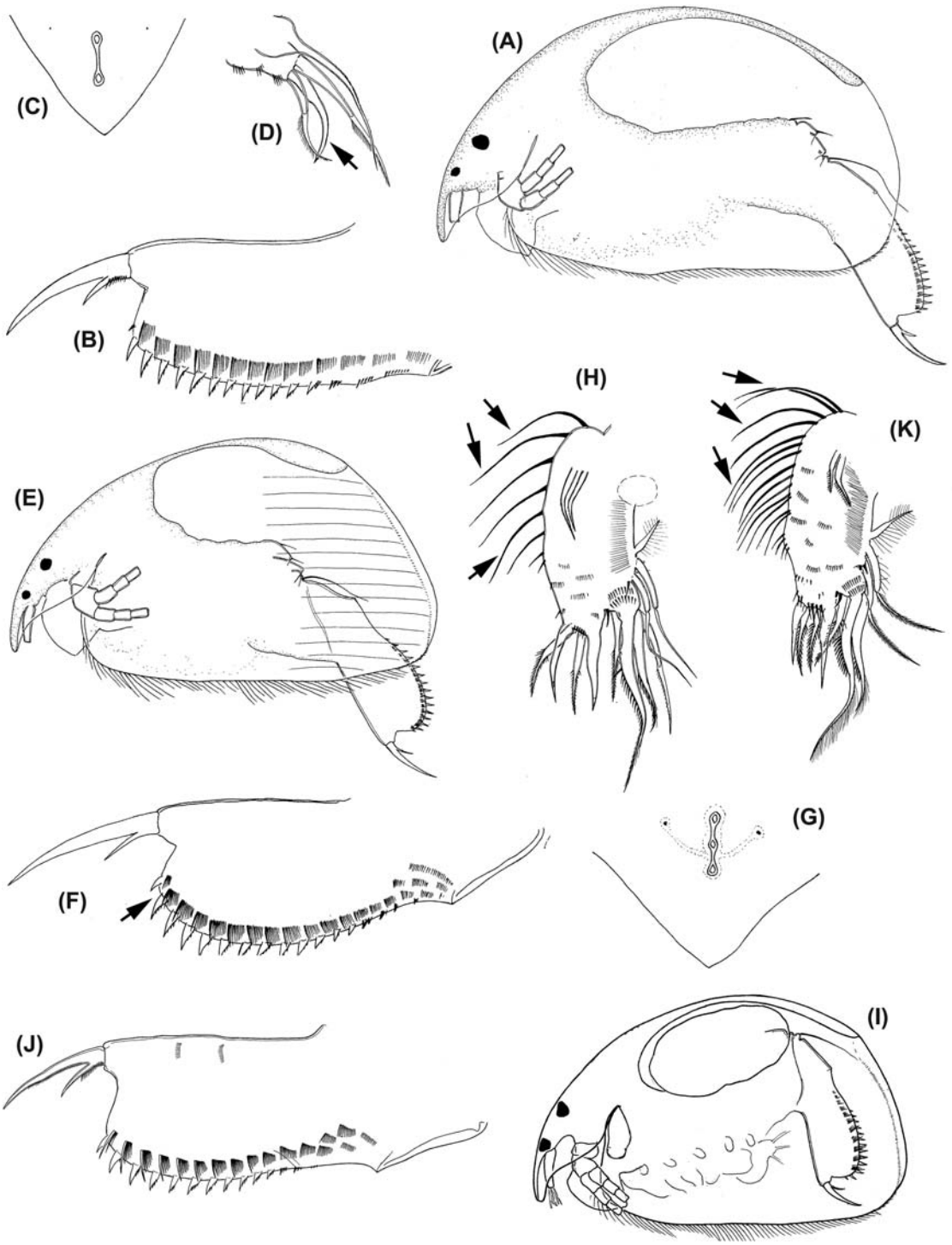


FIGURE 16.2.30 Representatives of Aloninae (Chydoridae): (A–D) *Alona affinis*, general view, postabdomen, head pores, and distal portion of limb I; (E–H) *Alona quadrangularis*, general view, postabdomen, head pores, limb I; (I–K) *Alona kotovi*, general view, postabdomen, and limb I.

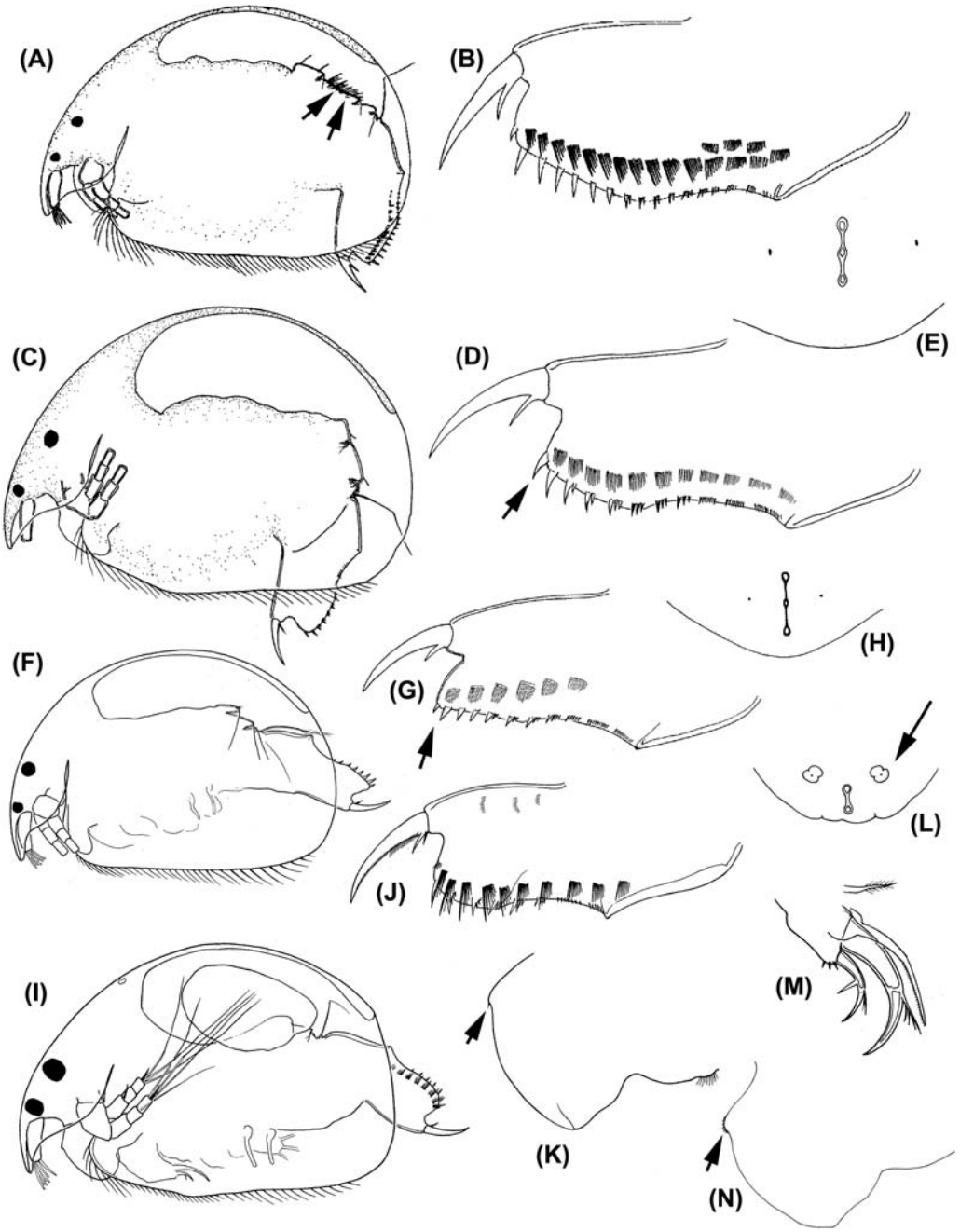


FIGURE 16.2.31 Representatives of Aloninae (Chydoridae): (A and B) *Alona setosocaudata*, general view and postabdomen; (C–E) *Alona werestschagini*, general view, postabdomen, and head pores; (F–H) *Alona guttata*, general view, postabdomen, and head pores; (I–M) *Anthalona harti*, general view, postabdomen, head pores, inner distal lobe of limb I and labrum; (N) *Anthalona mediterranea*, labrum; (N) *from Van Damme et al., 2011*.

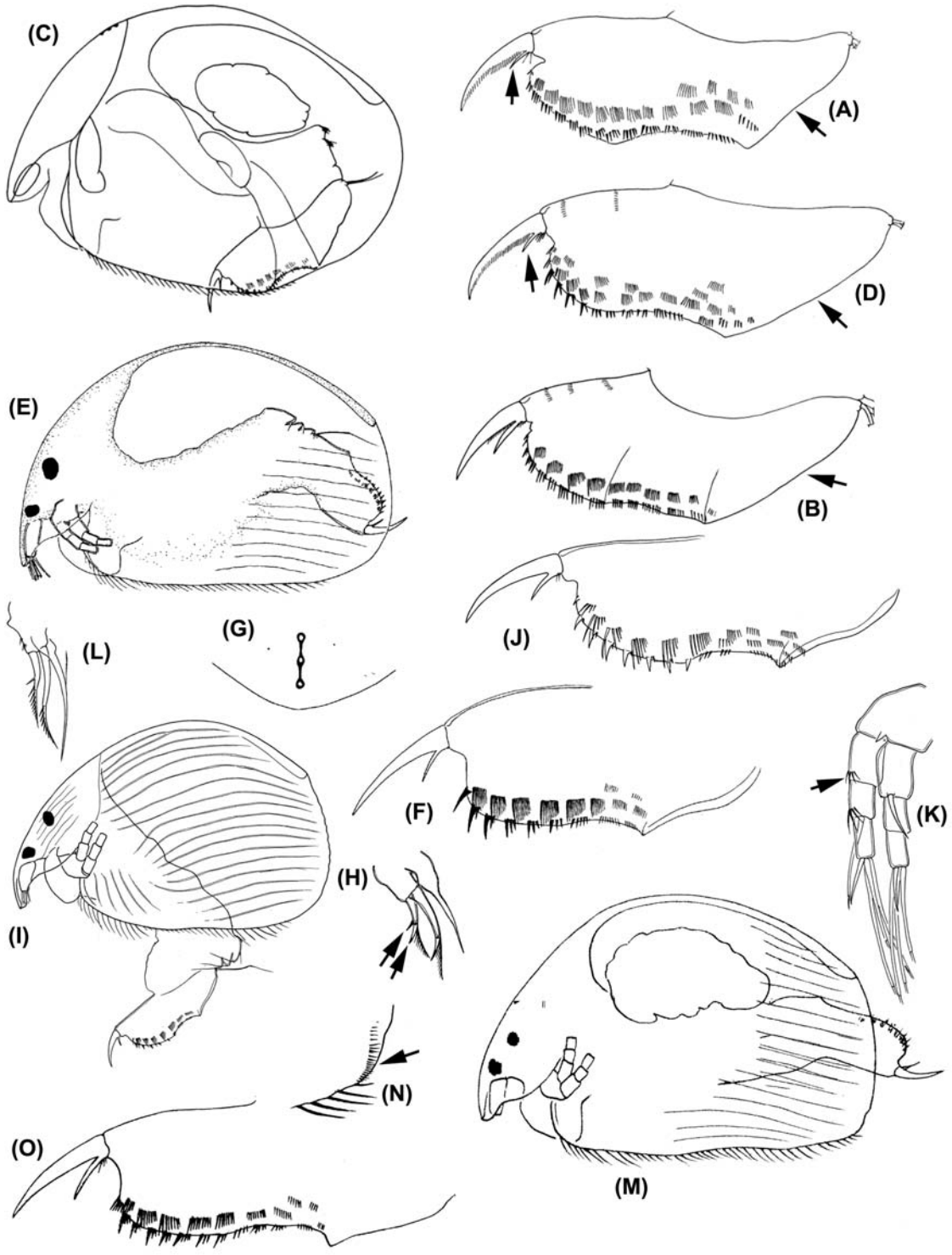


FIGURE 16.2.32 Representatives of Aloninae (Chydoridae): (A) *Brancelia sketi*, postabdomen; (B) *Brancelia stochi*, postabdomen; (C and D) *Brancelia hercegovinae*, general view and postabdomen; (E–H) *Coronatella rectangula*, general view, postabdomen, head pores, and inner distal lobe of limb I; (I–L) *Coronatella trachistriata*, general view, postabdomen, antenna II, and inner distal lobe of limb I; (M–O) *Coronatella anemae*, general view, postero-ventral angle of valve and postabdomen; (M–O) *redrawn from Van Damme & Dumont, 2008.*

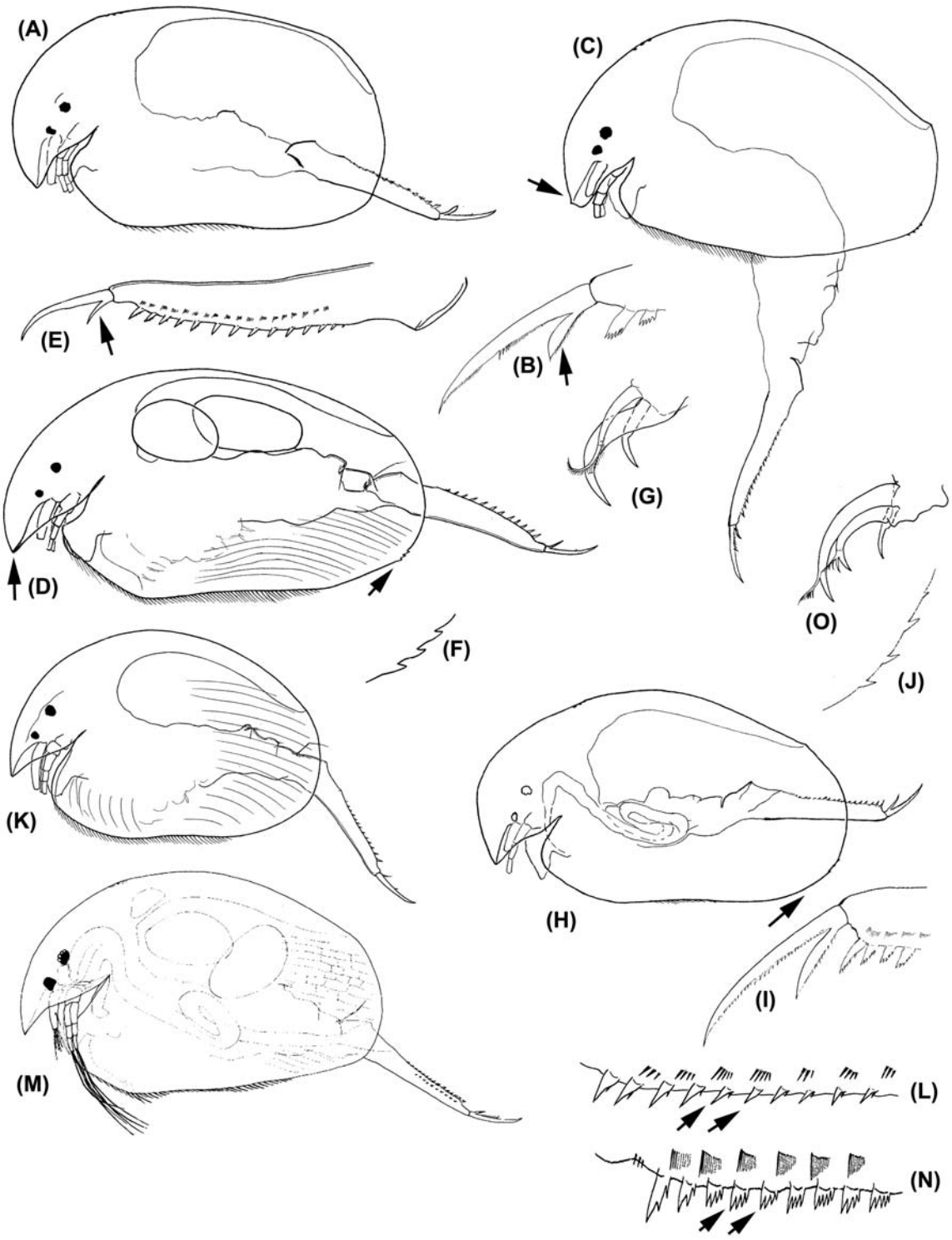


FIGURE 16.2.33 Representatives of Aloninae (Chydoridae): (A and B) *Camptocercus fennicus*, general view and postabdominal claw; (C) *Camptocercus lillejeborgi*, general view; (D–G) *Camptocercus rectirostris*, general view, postabdomen, postero-ventral angle of valves, inner distal lobe of limb I; (H–J) *Camptocercus streletskayae*, general view, postabdominal claw, postero-ventral angle of valves; (K and L) *Captocercus vietnamensis*, general view and marginal denticles of postabdomen; (M and O) *Camptocercus uncinatus*, general view, marginal denticles of postbdomen, and inner distal lobe of limb I.

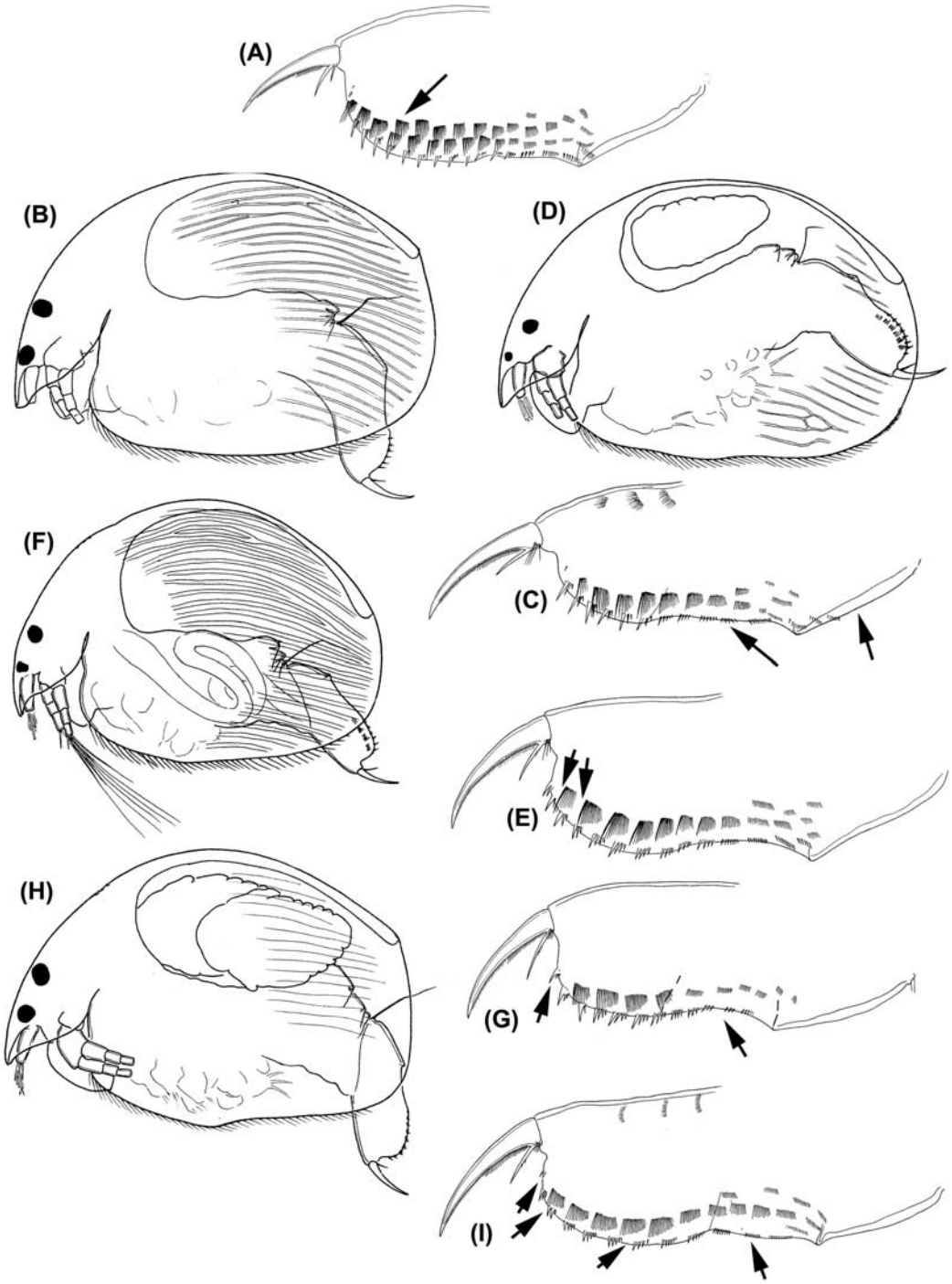


FIGURE 16.2.34 Representatives of Aloninae (Chydoridae): (A) *Alona orellanai*, postabdomen; (B and C) *Alona elegans*, general view and postabdomen; (D and E) *Alona salina*, general view and postabdomen; (F and G) *Alona irinae*, general view and postabdomen; (H and I) *Alona floessneri*, general view and postabdomen.

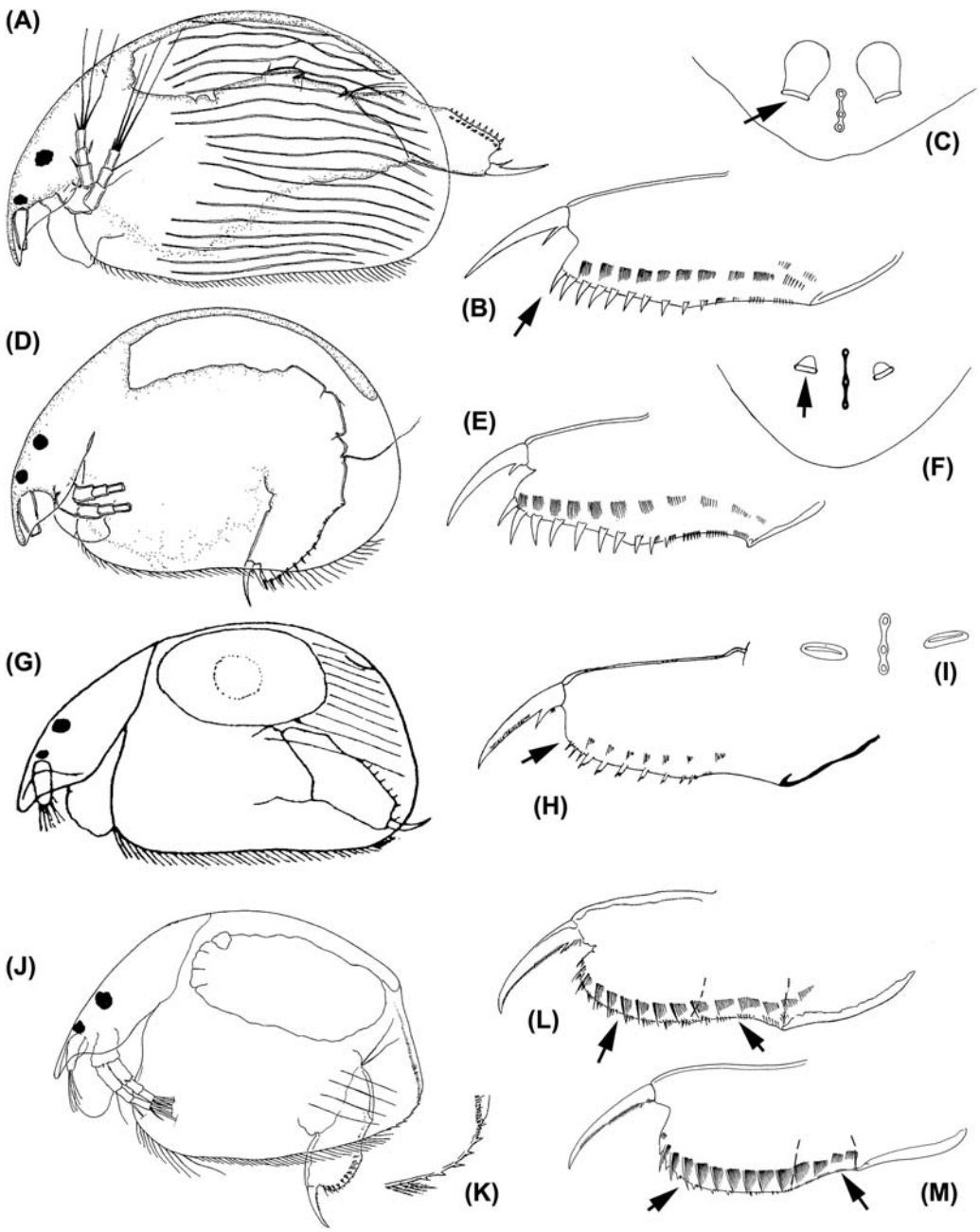


FIGURE 16.2.35 Representatives of Aloninae (Chydoridae): (A–C) *Flavalona costata*, general view, postabdomen, and head pores; (D–F) *Flavalona rustica*, general view, postabdomen and, head pores; (G–I) *Flavalona weltneri*, general view, postabdomen, and head pores; (J–L) *Karualona iberica*, general view, postabdomen, and postero-ventral angle of valves; (M) *Karualona karua*, postabdomen.

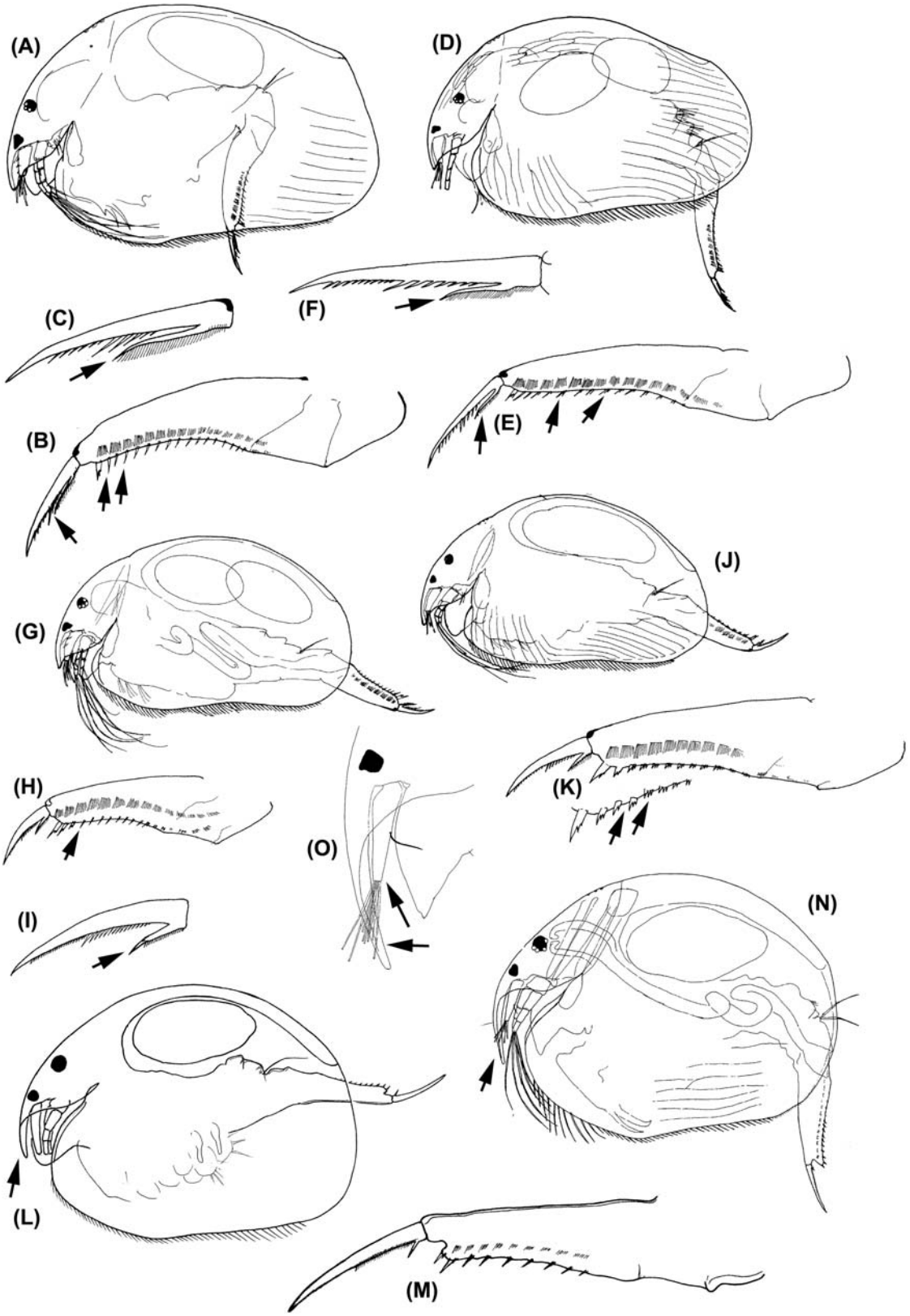


FIGURE 16.2.36 Representatives of Aloninae (Chydoridae): (A–C) *Kozhowia gajewskayae*, general view, postabdomen, and postabdominal claw; (D–F) *Kozhowia brevidentata*, general view, postabdomen, and postabdominal claw; (G–I) *Kozhowia primigenia*, G, general view, postabdomen, and postabdominal claw; (J and K) *Kozhowia kozhowi*, general view and postabdomen; (L and M) *Kurzia latissima*, general view and postabdomen; (N and O) *Kurzia longirostris*, general view and rostrum.

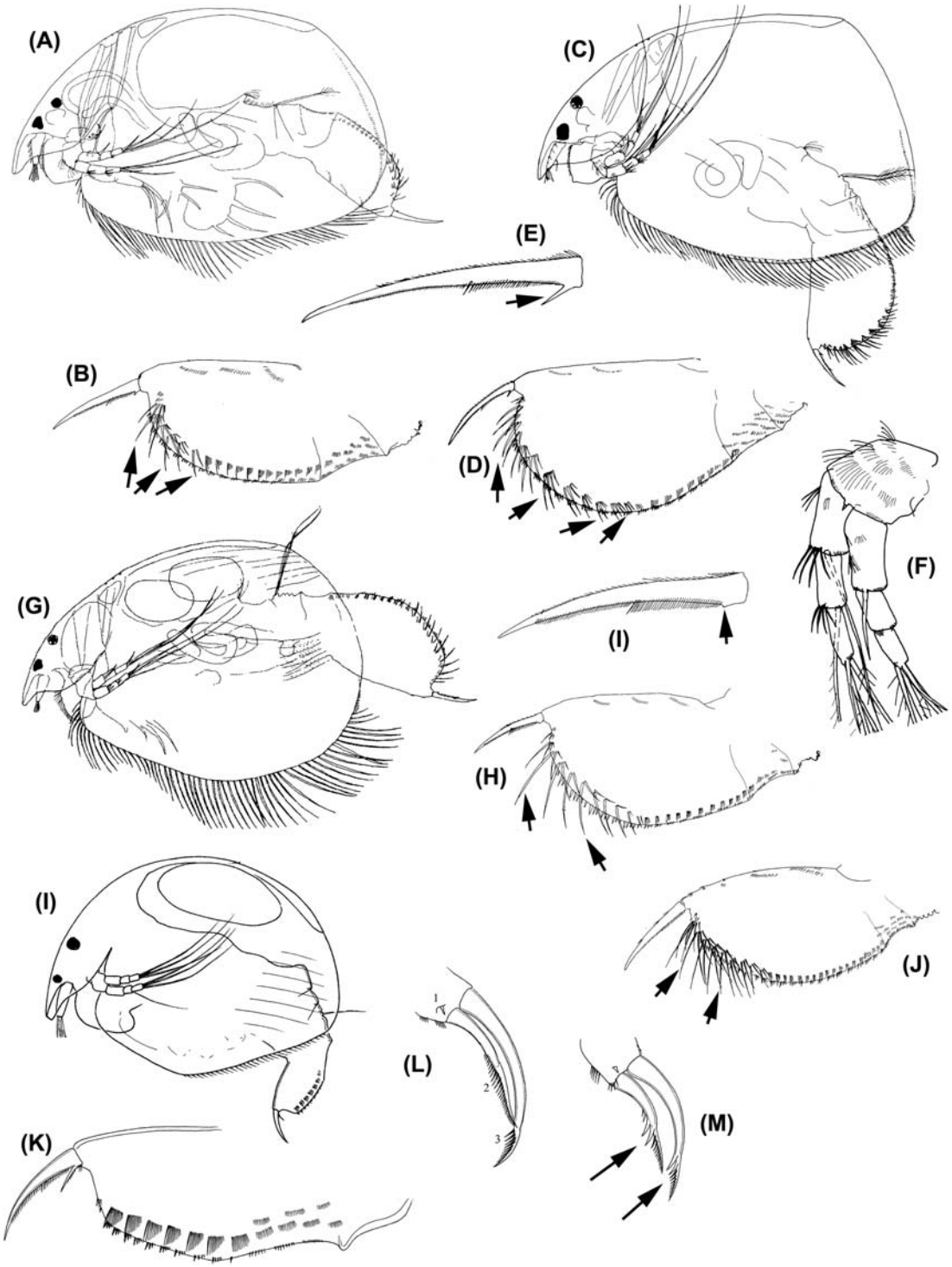


FIGURE 16.2.37 Representatives of Aloninae (Chydoridae): (A and B) *Leydigia korovchinskyi*, general view and postabdomen; (C–F) *Leydigia leydigi*, general view, postabdomen, postabdominal claw, and antenna II; (G–I) *Leydigia acanthocercoides*, general view, postabdomen, and postabdominal claw; (J) *Leydigia iberica*, postabdomen; (I–L) *Leberis diaphanus*, general view, postabdomen, and inner distal lobe of limb I; (M) *Leberis punctatus*, inner distal lobe of limb I.

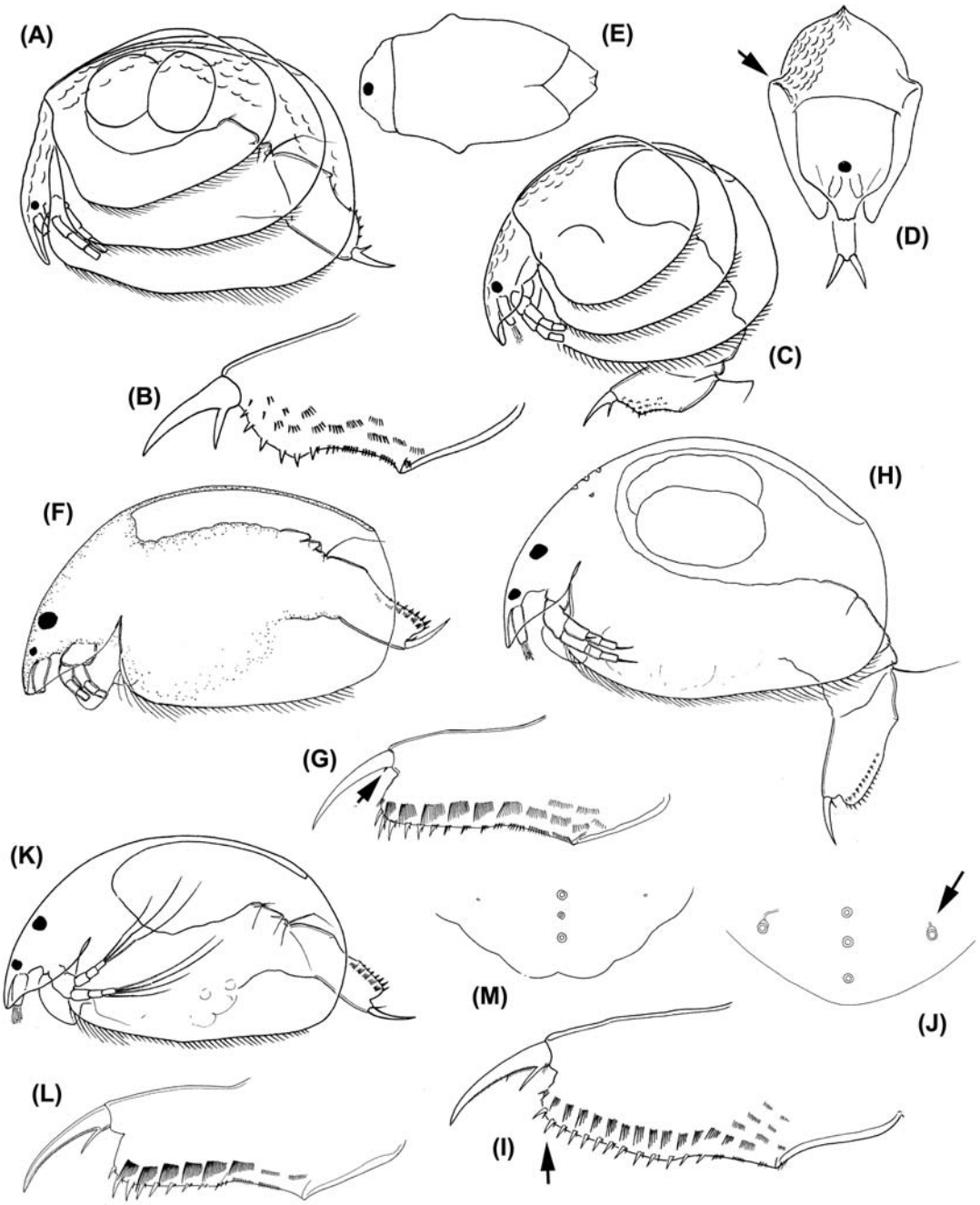


FIGURE 16.2.38 Representatives of Aloninae (Chydoridae): (A and B) *Monospilus dispar*, general view and postabdomen; (C–E) *Monospilus daedalus*, lateral, frontal and dorsal view; (F and G) *Ovalona karelica*, general view and postabdomen; (H–J) *Ovalona niragica*, general view, postabdomen, and head pores; (K–M) *Ovalona cambouei*, general view, postabdomen, and head pores.

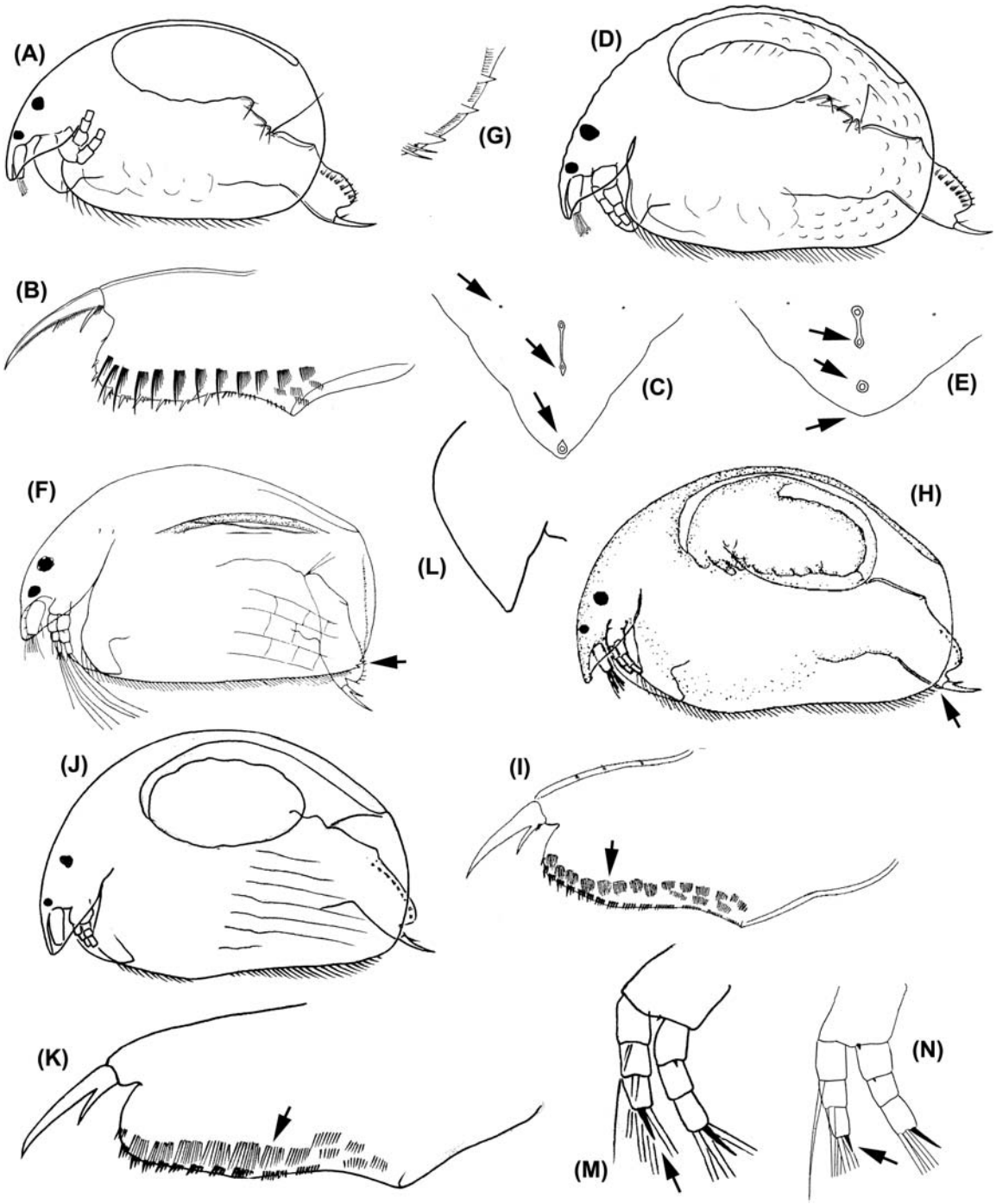


FIGURE 16.2.39 Representatives of Aloninae (Chydoridae): (A–C) *Ovalona azorica*, general view, postabdomen, and head pores; (D and E) *Ovalona anastasia*, general view and head pores; (F and G) *Phreatalona protzi*, general view and postro-ventral angle of valves; (H and I) *Phreatalona labrosa*, general view and postabdomen; (J–M) *Phreatalona phreatica*, general view, postabdomen, labrum, and antenna II; (N) *Phreatalona smirnovi*, antenna II; (J–M) *redrawn from Alonso, 1996;* (N) *redrawn from Van Damme et al., 2009.*

4′	Postabdomen lateral group distal setules as thin as others; limb I medial distal lobe with seta one very small, rudimentary; limb I anterior margin with clusters of numerous thin setules 6
5(4)	Limb I medial distal lobe with anterior margin bearing seven or eight large setules (Figs. 16.2.29 E–H) ..... *Alona quadrangularis* (O.F. Müller, 1785) [Widely distributed in Palaearctic]
5′	Limb I medial distal lobe with anterior margin bearing 12–14 large setules (Figs. 16.2.29 I–K) ..... *Alona kotovi* Sinev 2012 [South Korea]
6(4)	Postabdomen distal angle more or less round; body length to 0.55 mm; interpore distance = 0.9–1.0 postpore distance (Figs. 16.2.31 C–E) ..... *Alona werestschagini* Sinev, 1999 [Iceland, North Europe, the Pamirs, Tian Shan and Altai mountains, Kommander Islands]
6′	Postabdomen distal angle acute, protruding; body length to 0.45 mm; interpore distance = 0.25–0.35 postpore distance (Figs. 16.2.31 F–H) ..... *Alona guttata* Sars, 1862 [Widely distributed in Palaearctic]

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: Genera

1	Eye and ocellus not large; rosrum long to moderate; antenna I not projecting far beyond the rostrum apex 2
1′	Eye and ocellus exremely large; antenna I projecting far beyond very short rostrum apex (Fig. 16.2.40 A) ..... *Dadaya macrops* (Daday, 1898) [Subtropical Palaearctic]
2(1)	Head pores present; labral keel not serrated 3
2′	Head pores absent, labral keel serrated ..... ***Ephemeroporus*** **[p. 710]**
3(2)	Two primary head pores, lateral head pores situated on head shield midline 4
3′	One primary head pore, lateral head pores situated far from head shield midline (Figs. 16.2.40 B, C) ..... *Estateroporus gauthieri* Alonso, 1990 [Spain]
4(3)	Ventral valve margin posterior half with setae situated marginally or slightly submarginally 5
4′	Ventral valve margin posterior half with setae situated on the inner surface, set back from margin 8
5(4)	Body laterally compressed; valve accessory anterior flange not protruding beyond anterior margin 6
5′	Body globular; valve accessory anterior flange large, protruding beyond anterior margin (Figs. 16.2.40 D–F) ..... *Paralona pigra* (Sars, 1862) [Temperate Palaearctic]
6(5)	Posterior valve margin breadth about half of body breadth or more 7
6′	Posterior valve margin breadth about third of body breadth ..... ***Pleuroxus*** **[p. 712]**
7(6)	Body high, rounded; distance from rostrum apex to antenna I apex less than length of antenna I ..... ***Alonella*** **[p. 713]**
7′	Body low, oval; distance from rostrum apex to antenna I apex greater than length of antenna I ..... ***Disparalona*** **[p. 713]**
8(4′)	Valve ventral margin without an incurvation 9
8′	Valve ventral margin with large, medial incurvation, followed by an acute process (Figs. 16.2.40 G) ..... *Anchistropus emarginatus* Sars, 1862 [Temperate Palaearctic]
9(8)	Labrum with keel; postabdomen short or of moderate length 10
9′	Labrum without keel; postabdomen long and narrow (Figs. 16.2.40 H–J) ..... *Pseudochydorus globosus* (Baird, 1843) [Palaearctic]
10(9)	Postabdomen very broad distally, but concave in anal/preanal portion (Figs. 16.2.40 K, L) ..... *Dunhevedia crassa* King, 1853 [Palaearctic]
10′	Postabdomen subrectangular distally and with a prominent preanal angle ..... ***Chydorus*** **[p. 713]**

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: *Ephemeroporus:* Species

1	Valve posterioventral angle with denticles 2
1′	Valve posterioventral angle without denticles (Figs. 16.2.43 K–N) ..... *Ephemeroporus phintonicus* (Margaritora, 1969) [Algeria, France, Sardinia]
2(1)	Labral keel with rounded apex 3

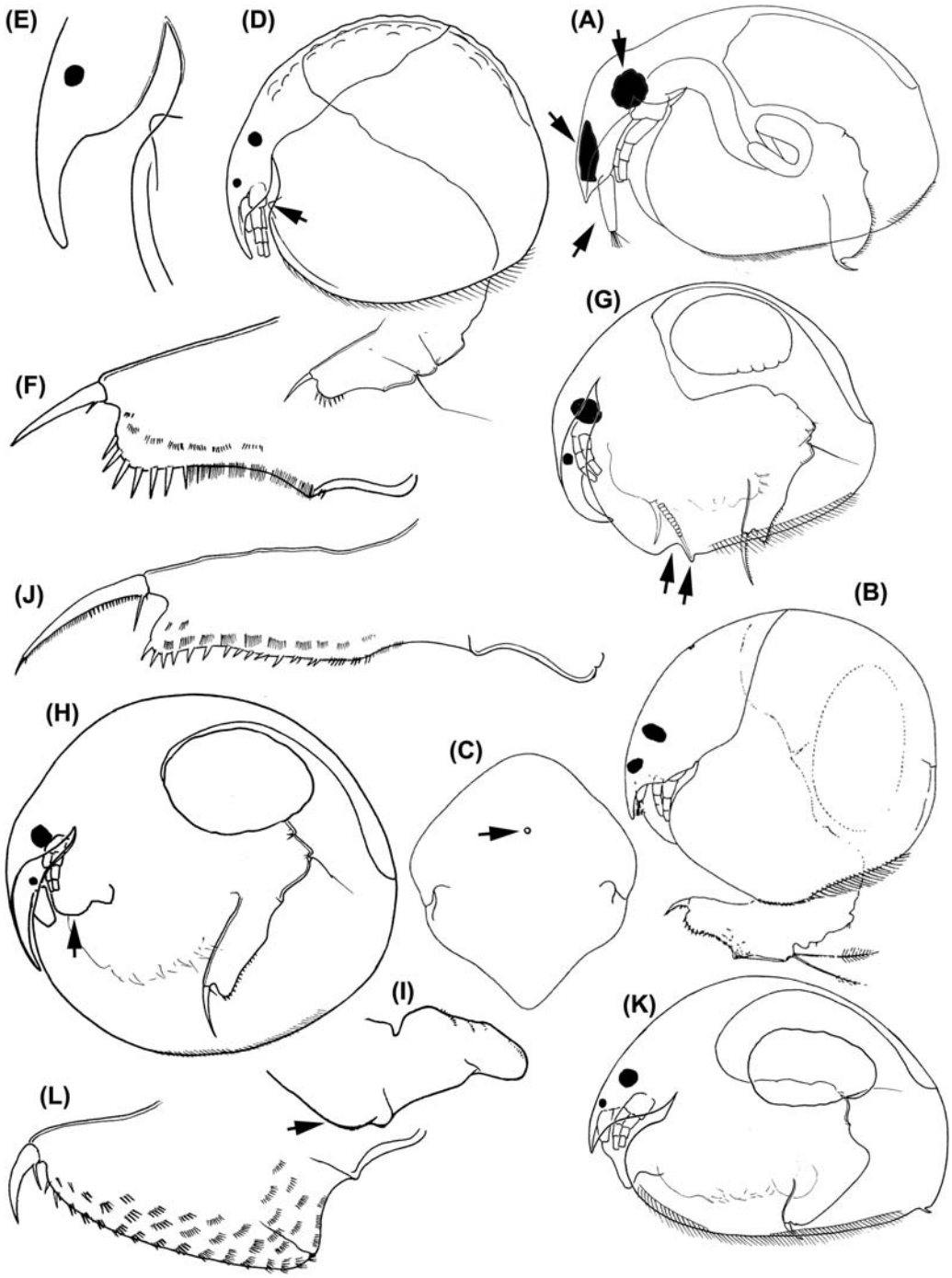


FIGURE 16.2.40 Representatives of Chydorinae (Chydoridae): (A) *Dadaya macrops*, general view; (B and C) *Estateroporus gauthieri*, general view and head shield; (D–F) *Paralona pigra*, general view, anterior margin of valve, and postabdomen; (G) *Anchistropus emarginatus*, general view; (H–J) *Pseudochydorus globosus*, general view, labrum and postabdomen; (K and L) *Dunhevedia crassa*, general view and postabdomen.

2′	Labral keel with acute apex (Figs. 16.2.44 A–C)	*Ephemeroporus epiaphantoii* Alonso, 1987 [Spain]
3(2)	Labral keel apex wide, broadly rounded (Figs. 16.2.44 D, E)	*Ephemeroporus margalefi* Alonso, 1987 [Spain]
3′	Labral keel apex narrow, rounded only apically (Figs. 16.2.33 F–H)	*Ephemeroporus barroisi* (Richard, 1894) [southern Palearctic. Pantropical. Possibly a species group]

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: *Pleuroxus*: Species

1	Valves with lateral projections	2
1′	Valves without lateral projections	3
2(1)	Postabdominal postanal teeth large, mainly singular; antenna II exopod basal article with spine longer than half of second article (Figs. 16.2.44 I–L)	*Pleuroxus pamirensis* (Werestschagin, 1923) [Pamir mountains]
2′	Postabdominal postanal teeth small, mainly grouped; postabdomen preanal margin shorter than anal margin; antenna II exopod basal article with spine shorter than 50% length of second article (Figs. 16.2.44 M–O)	*Pleuroxus annandalei* (Daday, 1908) [Tibetan plateau, Baikal rift system, Mongolian Altai]
3(1)	Valve posterior margin without denticles	4
3′	Valve posterior margin with numerous denticles (Fig. 16.2.45 A)	*Pleuroxus truncatus* (O.F. Müller, 1785) [Palaearctic]
4(3)	Rostrum apex curved ventrally or posteriorly	5
4′	Rostrum apex curved anteriorly (Figs. 16.2.45 B, C)	*Pleuroxus uncinatus* Baird, 1850 [Palaearctic]
5(4)	Body almost circular in lateral view	6
5′	Body oval in lateral view	8
6(5)	Rostrum short, less than twice as long as antenna I; valves without a dorsal, sharp, medial keel	7
6′	Rostrum long, three times longer than antenna I; valves with a dorsal, sharp, medial keel (Figs. 16.2.45 D, E)	*Pleuroxus smirnovi* Kotov, 2008 [Pamirs]
7(6)	Postabdomen with two rows of lateral fascicles of setae (Figs. 16.2.45 F, G)	*Pleuroxus letourneuxi* (Richard, 1888) [Mediterranean]
7′	Postabdomen with one row of lateral fascicles of setae (Figs. 16.2.45 H, I)	*Pleuroxus jejuensis* Jeong, Kotov & Lee, 2013 [South Korea (Jeju Island)]
8(5)	Postabdominal distal denticles significantly larger that others	9
8′	Postabdominal denticles gradually decrease in size proximally	11
9(8)	Postabdomen weakly narrowing distally, length of postanal part about 2.5 times or less its breadth at level of distal angle	10
9(8)	Postabdomen strongly narrowing distally, length of its postanal part more than three times greater than its breadth at level of distal angle (Figs. 16.2.45 J–L)	*Pleuroxus laevis* (Sars, 1862) [Palaearctic]
10(9)	Valves with obvious linear sculpture; postabdomen with most postanal denticles with small spine clusters near their bases (Figs. 16.2.46 A–C)	*Pleuroxus denticulatus* (Birge, 1879) [Central Europe]
10′	Valves without sculpture; postabdomen postanal denticles without spine clusters near their bases (Figs. 16.2.46 D–F)	*Pleuroxus trigonellus* (O.F. Müller, 1785) [Palaearctic]
11(8)	Valve posterioventral angle with denticles	12
11′	Valve posterioventral angle without denticles (Figs. 16.2.46 G, H)	*Pleuroxus pigroides* Lilljeborg, 1900 [Russia, Sweden]
12(11)	Postabdomen not very long and narrow, length of distal (anal+postanal) part less than three times greater than length of preanal part	13
12′	Postabdomen very long and narrow, length of its distal (anal+postanal) part more than four times greater than length of preanal part (Figs. 16.2.46 I–K)	*Pleuroxus striatus* (Shödler, 1863) [Temperate Palaearctic]

13(12) Postabdomen preanal part subequal or slightly longer than anal part (Figs. 16.2.46 L–N) ..... *Pleuroxus aduncus* (Jurine, 1820) [Palaearctic]

13′ Postabdomen preanal part at least 1.5 times longer than anal part (Figs. 16.2.46 O–Q) .... *Pleuroxus quasidenticulatus* (Smirnov, 1996) [China, Iran, Russia]

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: *Alonella*: Species

1 Body oval in lateral view, with ventral margin weakly convex to straight; valve sculpture polygons and anastomosing lines 2

1′ Body subglobular, with ventral margin evenly convex; valve sculpture curved diagonal, nonanastomosing lines (Figs. 16.2.41 A, B) .... *Alonella nana* (Baird, 1850) [Palaearctic]

2(1) Valves with obvious striae within polygons (Figs. 16.2.41 C–E) ..... *Alonella excisa* (Fischer, 1854) [Palaearctic]

2′ Valves without striae in polygons (Figs. 16.2.41 F, G) ..... *Alonella exigua* (Lilljeborg, 1901) [Widely distributed in Palaearctic]

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: *Disparalona*: Species

1 Valves with lateral folds 2

1′ Valves without lateral folds 3

2(1) Valve lateral projections strong and sharp (Figs. 16.2.43 A–C) ..... *Disparalona ikarus* Kotov & Sinev, 2011 [China, Russia, South Korea]

2′ Lateral projections on valves low and rounded ..... *Disparalona leei* Chien, 1970 species group [Europe, Siberia]

3(1) Postabdominal claw with two basal spines 4

3′ Postabdominal claw with one basal spine (Figs. 16.2.43 D, E) ..... *Disparalona rostrata* (Koch, 1841) [Temperate Palaearctic]

4(3) Labral plate small, its breadth subequal to length of antenna I (Figs. 16.2.43 F–H) .....*Disparalona smirnovi* Sinev, 2016 [Siberia]

4′ Labral plate large, its breadth 2–3 times longer than antenna I (Figs. 16.2.43 I, J) ..... *Disparalona chappuisi* (Brehm, 1934) [China, South Korea]

Branchiopoda: Anomopoda: Chydoridae: Chydorinae: *Chydorus*: Species

1 Postabdomen preanal margin smooth 2

1′ Postabdomen preanal margin with numerous small protrusions (Figs. 16.2.41 H, I) ..... *Chydorus pizarri* Alonso, 1984 [Spain]

2(1) Valves without lateral outgrowths 3

2′ Valves with obvious lateral outgrowths (Figs. 16.2.42 A–C) ..... *Chydorus irinae* Smirnov & Sheveleva, 2010 [Russia, South Korea]

3(2) Body globular or subglobular, not humpbacked 4

3′ Body humpbacked (Figs. 16.2.41 J, K) ..... *Chydorus gibbus* Sars, 1891 [Temperate regions of Palaearctic]

4(3) Antenna I without lateral aesthetasc; antenna II exopod basal article without seta 5

4′ Antenna I with lateral aesthetasc; antenna II exopod basal article with seta (Figs. 16.2.42 D–G) ..... *Chydorus ovalis* Kurz, 1875 [Temperate Palaearctic]

5(4) Postabdomen anal teeth more or less regularly distributed in preanal and anal margins 6

5′ Postabdomen anal teeth concentrated in region of dorsodistal angle (Figs. 16.2.42 H, I) .... *Chydorus baikalensis* Smirnov & Sheveleva, 1996 [Lake Baikal]

6(5) Ephippium with two eggs ..... *Chydorus biovatus* Frey, 1985 [Russia (Kamchatka Peninsula)]

6′ Ephippium with one egg (Figs. 16.2.42 J–L) ..... *Chydorus sphaericus* (O. F. Müller, 1785) species group [Cosmopolitan]

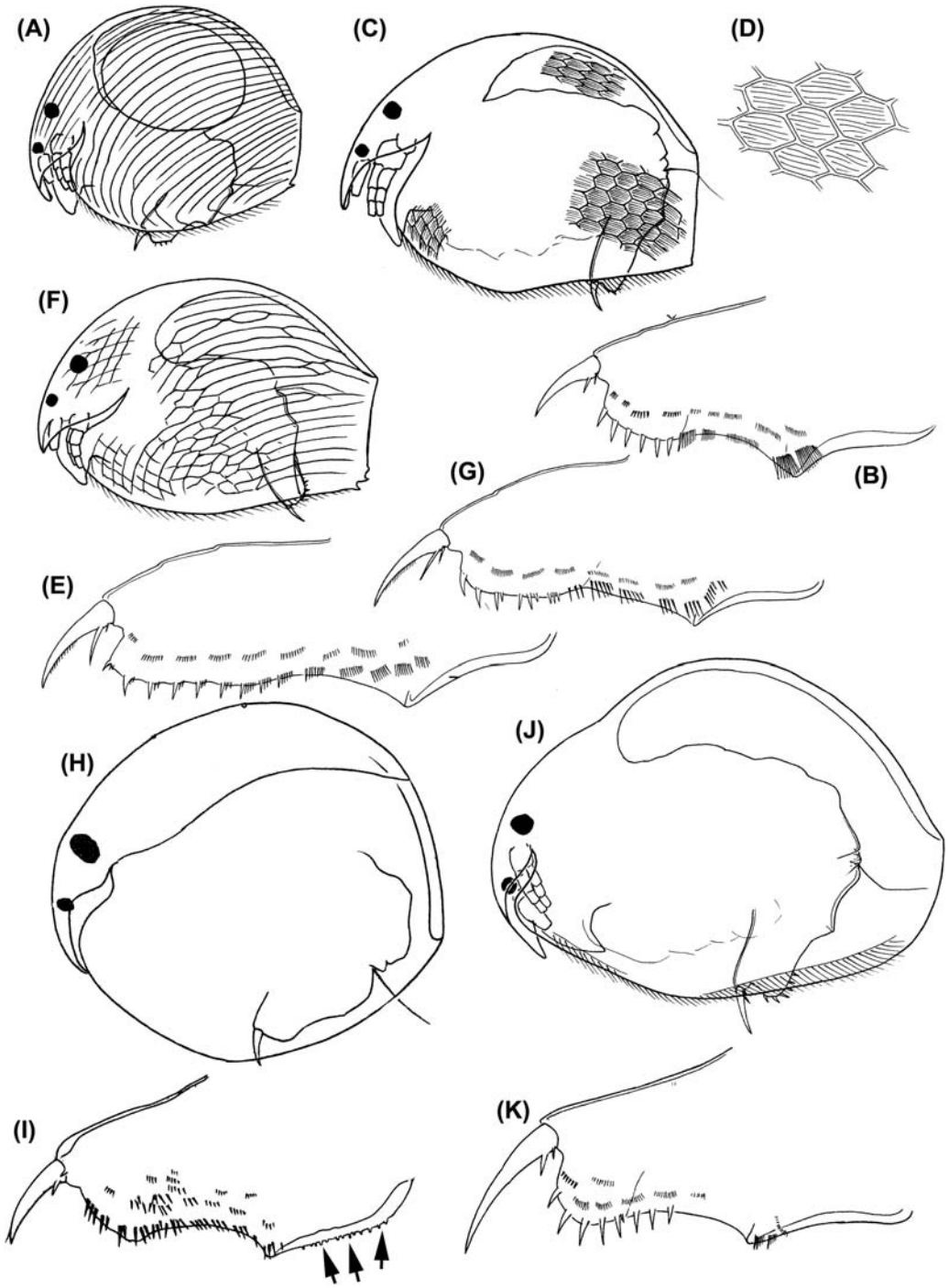


FIGURE 16.2.41 Representatives of Chydorinae (Chydoridae): (A and B) *Alonella nana*, general view and postabdomen; (C–E) *Alonella excisa*, general view, sculpture of valves, and postabdomen; (F and G) *Alonella exigua*, general view and postabdomen; (H and I) *Chydorus pizzari*, general view and postabdomen; (J and K) *Chydorus gibbus*, general view and postabdomen. *(H and I) Redrawn from Alonso (1996).*

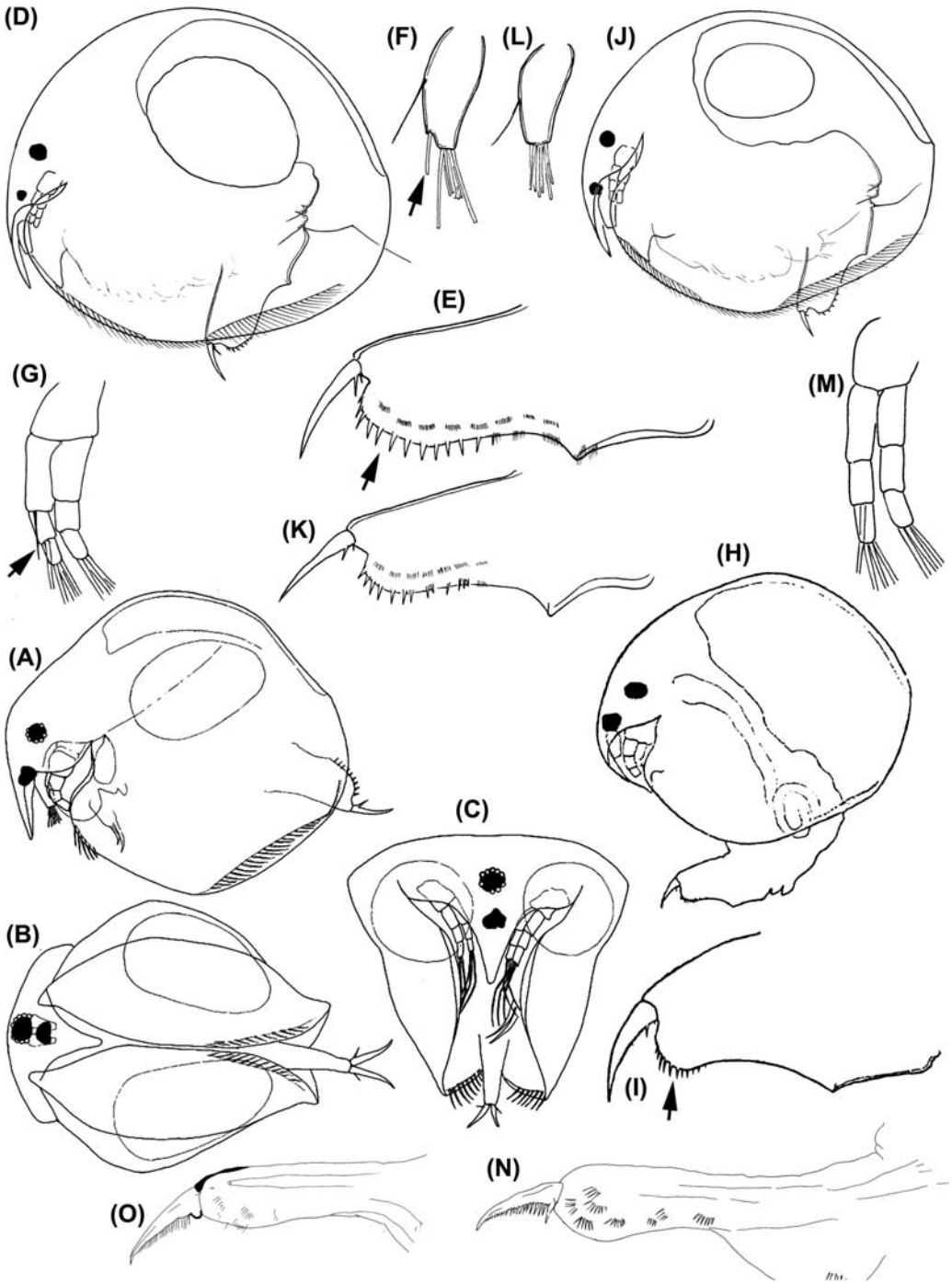


FIGURE 16.2.42 Representatives of Chydorinae (Chydoridae): (A–C) *Chydorus irinae*, lateral, ventral, and frontal view; (D–G) *Chydorus ovalis*, general view, postabdomen, antenna I, and antenna II; (H and I) *Chydorus baikalensis*, general view and postabdomen; (J–O) *Chydorus sphaericus*, general view, female postabdomen, antenna I, antenna II and male postabdomen; (N) *Chydorus belyaevae*, male postabdomen.

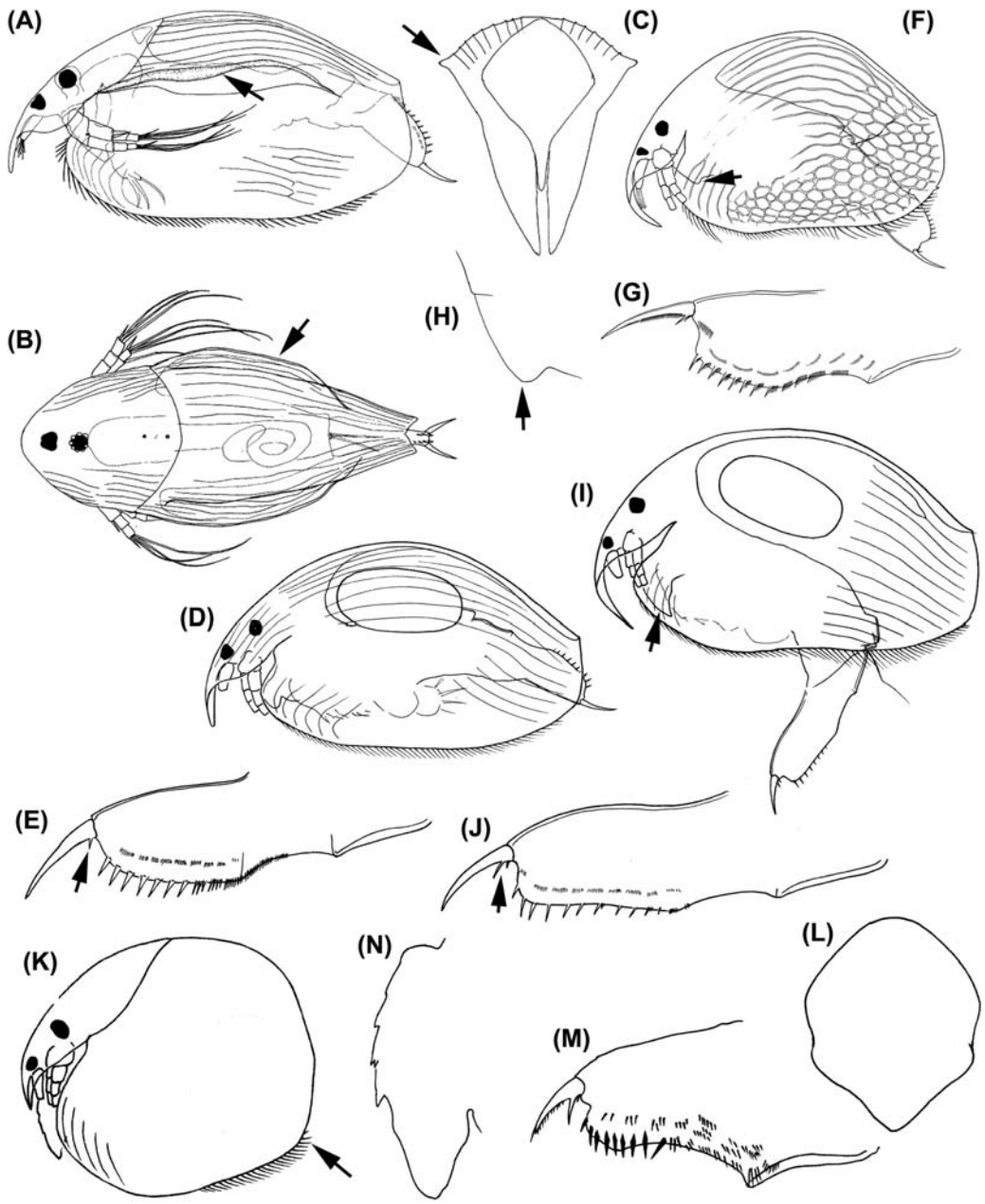


FIGURE 16.2.43 Representatives of Chydorinae (Chydoridae): (A–C) *Disparalona ikarus*, lateral, dorsal and frontal view; (D and E) *Disparalona rostrata*, general view and postabdomen, (F–H) *Disparalona acutirostris*, general view, postabdomen, and labrum; (I and J) *Disparalona chappuisi*, general view and postabdomen; (K–N) *Ephemeroporus phintonicus*, general view, head shield, postabdomen, and labrum. *(K–N) Redrawn from Alonso (1996).*

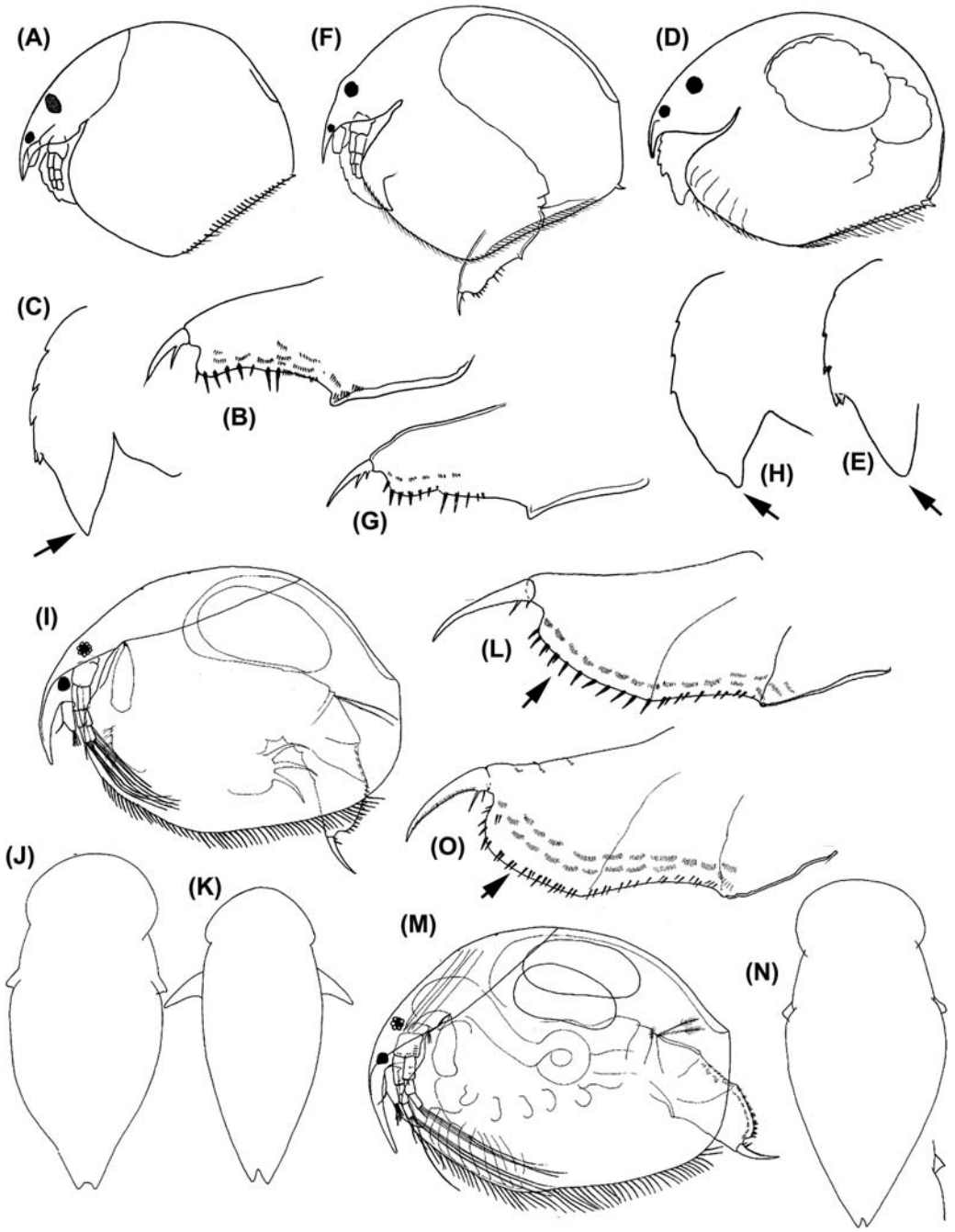


FIGURE 16.2.44 Representatives of Chydorinae (Chydoridae): (A–C) *Ephemeroporus epiaphantoii*, general view, postabdomen, and labrum; (D and E) *Ephemeroporus margalefi*, general view and labrum; (F–H) *Ephemeroporus barroisi*, general view, postabdomen, and labrum; (I–L) *Pleuroxus pamirensis*, lateral view, dorsal view, and postabdomen; (M–O) *Pleuroxus annandalei*, lateral view, dorsal view, and postabdomen. *(A–E) Redrawn from Alonso (1996).*

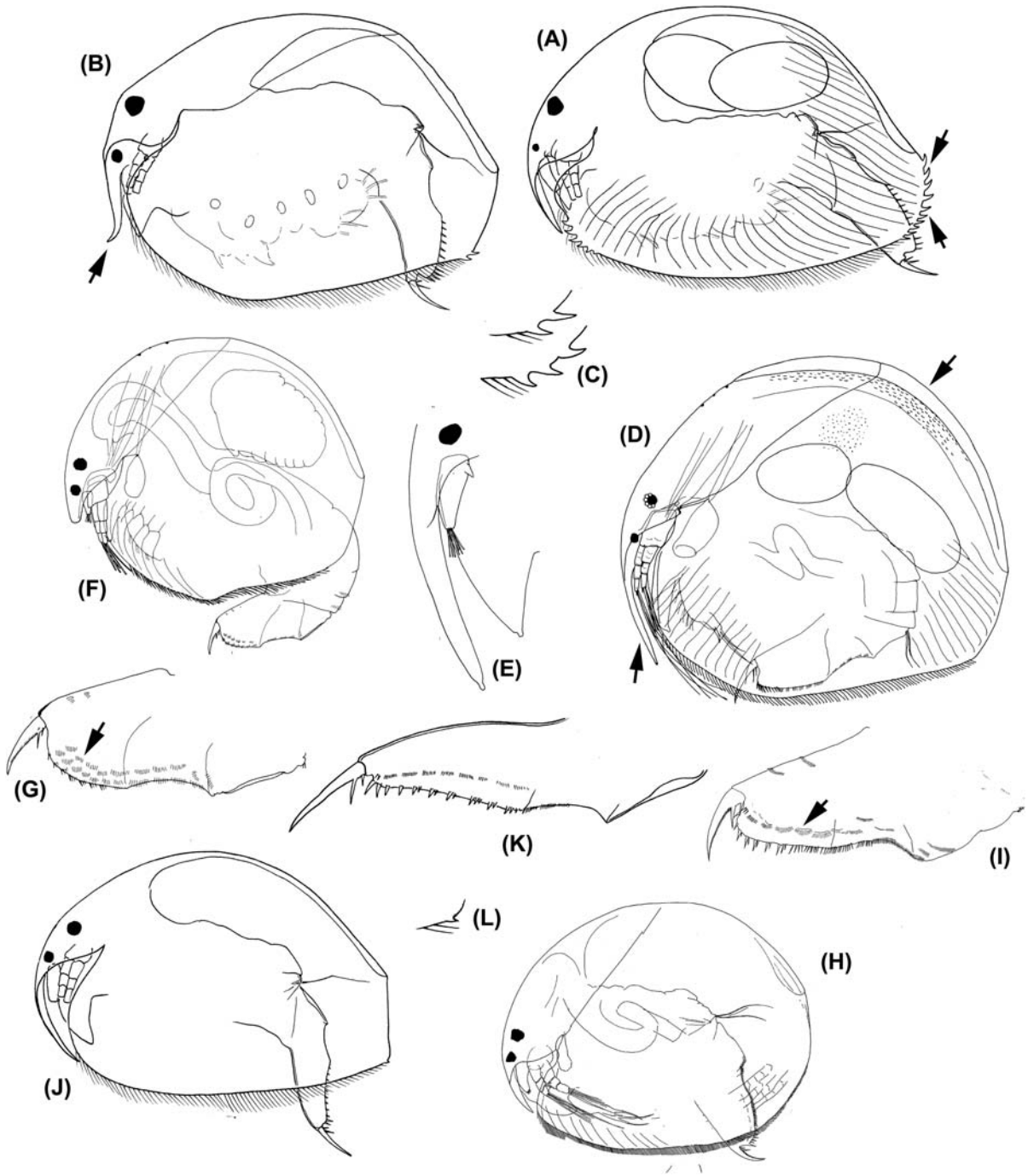


FIGURE 16.2.45 Representatives of Chydorinae (Chydoridae): (A) *Pleuroxus truncatus*, general view; (B and C) *Pleuroxus uncinatus*, general view and posteroventral angle of valves; (D and E) *Pleuroxus smirnovi*, general view and rostrum; (F and G) *Pleuroxus letourneuxi*, general view and postabdomen; (H and I) *Pleuroxus jejuensis*, general view and postabdomen; (J–L) *Pleuroxus laevis*, general view, postabdomen, and posteroventral angle of valves.

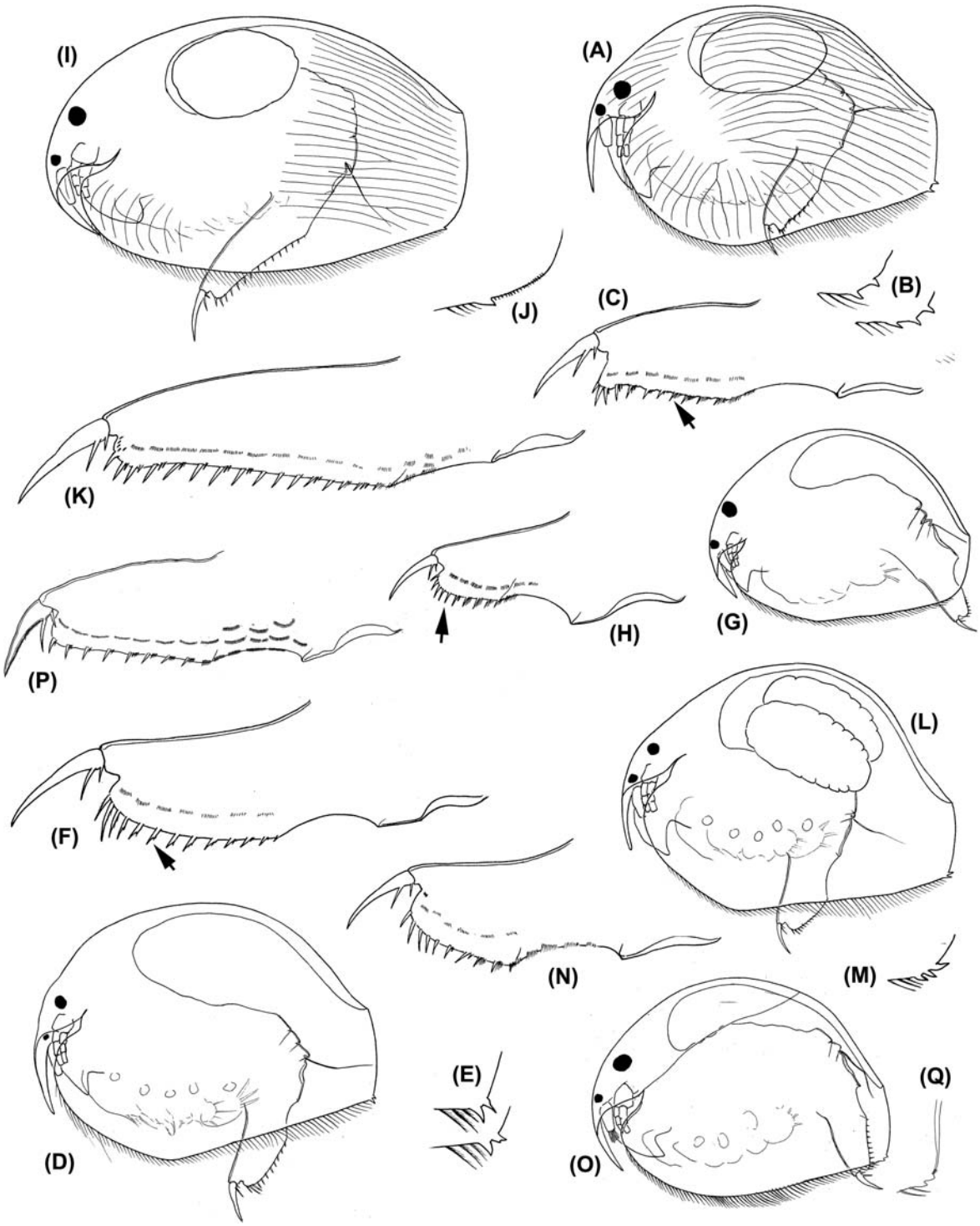


FIGURE 16.2.46 Representatives of Chydorinae (Chydoridae): (A–C) *Pleuroxus denticulatus*, general view, posteroventral angle of valves, and postabdomen; (D–F) *Pleuroxus trigonellus*, general view, posteroentral angle of valves, and postabdomen; (G and H) *Pleuroxus pigroides*, general view and postabdomen; (I–K) *Pleuroxus striatus*, general view, posteroventral angle of valves, and postabdomen; (L–N) *Pleuroxus aduncus*, general view, posteroventral angle of valves, and postabdomen; (O–Q) *Pleuroxus quasidenticulatus*, general view, posteroventral angle of valves, and postabdomen.

Branchiopoda: Cladocera: Onychopoda: Families

1	Abdominal and postabdominal (caudal) body parts greatly reduced 2
1′	Abdominal and postabdominal (caudal) body parts developed, the latter with long tail spine ..... **Cercopagididae [p. 720]**
2(1)	Postabdominal basal setae short ..... **Podonidae [p. 720]**
2′	Postabdominal basal setae long ..... Polyphemidae, one species: *Polyphemus pediculus* (Linnaeus, 1761) species group [Holarctic. In need of revision]

Cladocera: Onychopoda: Cercopagididae: Genera

1	Antenna II exopodite (upper branch) with eight setae, endopodite with seven setae; eye pigmental spot large, occupies about half of eye (Fig. 16.2.47 A) ..... ***Bythotrephes*** [Palaearctic. Invasive elsewhere]
1′	Both antenna II branches with seven setae; eye pigmental spot small (Fig. 16.2.47 B) ..... *Cercopagis pengoi* (Ostroumov, 1891) [Ponto-Caspian. Invasive elsewhere]

Onychopoda: Cercopagididae: *Bythotrephes*: Species

1	Postabdomen claws and tail spine not long and massive, apical end not curved; tail spine always straight without denticulated curvature 2
1′	Postabdomen claws and tail spine normally long and massive, apically curved anteriorly; tail spine long and usually possesses a prominent denticulated curvature (Figs. 16.2.47 C–E) ..... *Bythotrephes cederströmii* Schödler, 1877 [Northern Palaearctic Invasive elswhere]
2(1)	Adults with two or three claw pairs; limb I not very long, comparatively short, endopodite second segment apical setae well developed 3
2′	Adults with two pairs of straight claws situated closely on postabdomen and tail spine; limb I 80–132% of body length; endopodite second segment apical setae reduced or absent (Figs. 16.2.47 F–H) ..... *Bythotrephes longimanus* Leydig, 1860 [Europe]
3(2)	Adult body length 2.3–6.1 mm; tail spine 80–216% body length, thick basally; postabdomen claws and tail spine long, stout, inserted closely, curved posteriorly 4
3′	Adult body length 1.2–2.6 mm; tail spine 120–306% body length, thin basally; postabdomen claws and tail spine short, inserted rather sparsely, straight, directed either posteriorly or ventrally 5
4(3)	Tail spine basal width 5.5–15.0% body length; postabdomen claws and tail spine 4.5–19.0% body length, inserted comparatively sparsely (Fig. 16.2.47 J)..... *Bythotrephes arcticus* Lilljeborg, 1901 [Arctic and Subarctic Palaearctic]
4′	Tail spine basal width 4.4–7.0% body length; postabdomen claws and tail spine 5.0–11.0 body length, inserted comparatively densely (Fig. 16.2.47 K) ..... *Bythotrephes transcaucasicus* Behning, 1941 [Turkey, Armenia, Georgia]
5(4)	Postabdomen claws and caudal process 0.8–8.0% body length, directed posteriorly (Fig. 16.2.47 I) ..... *Bythotrephes brevimanus* Lilljeborg, 1901 [Europe]
5′	Postabdomen claws and caudal process 5.4–12.0% body length, directed ventrally ..... *Bythotrephes lilljeborgi* Korovchinsky, 2018 [Sweden, Norway]

Cladocera: Onychopoda: Podonidae: Genera

1	Head rounded, without outgrowth or horns (Figs. 16.2.47 C, D) ..... *Podonevadne trigona* (Sars, 1897) [Ponto-Caspian. Invasive elsewhere]
1′	Head with dorsal outgrowth and/or horns ..... ***Cornigerius***

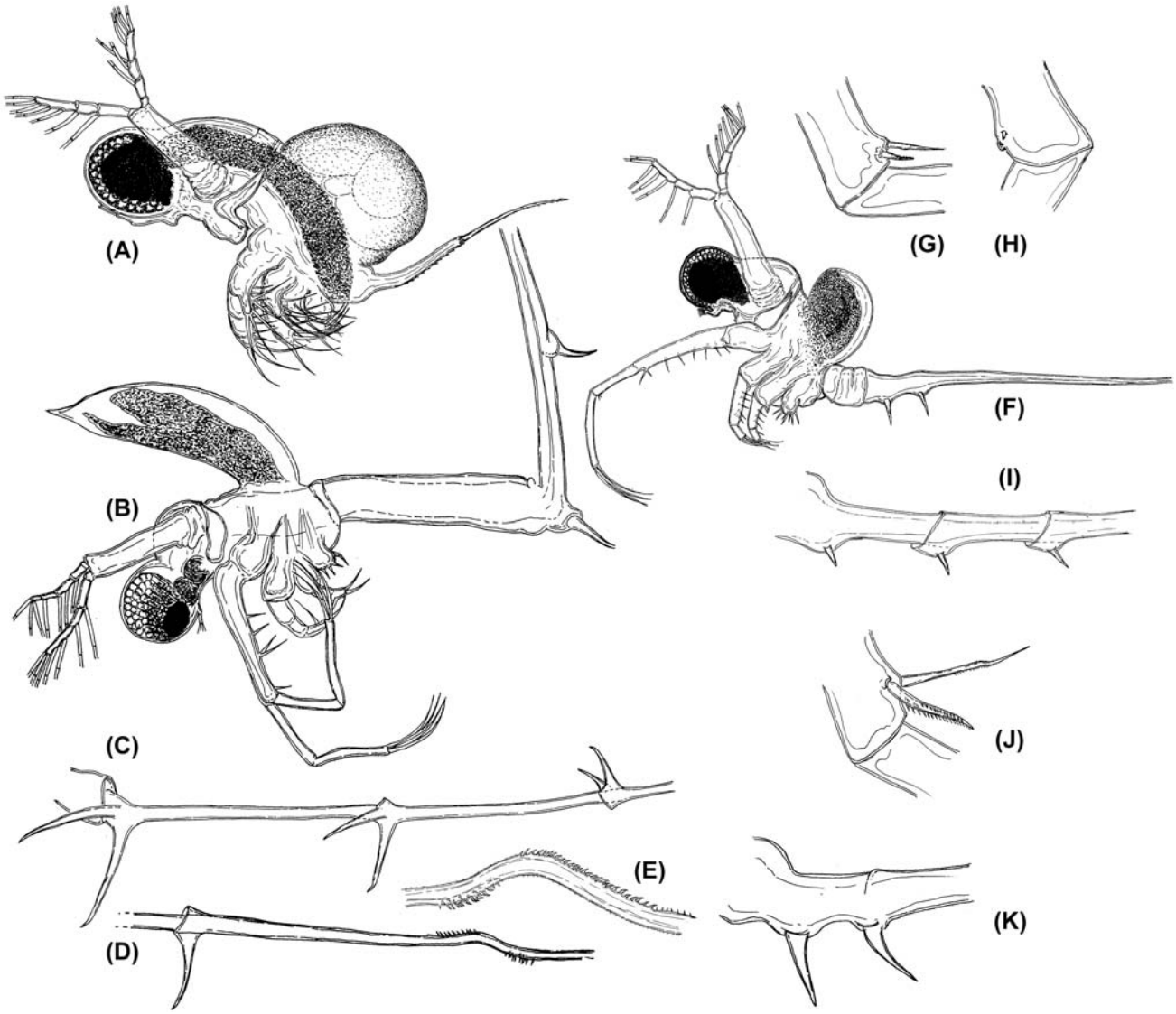


FIGURE 16.2.47 Representatives of Onychopoda (A–K): (A) *Polyphemus pediculus*; (B) *Cercopagis pengoi*; (C–E) *Bythotrephes cederströmii*, claws of postabdomen and tail spine, curvature of tail spine and denticulated curvature; (F–H) *Bythotrephes longimanus*, general view and distal setae of second endopodital segment of limb I; (I) *Bythotrephes brevimanus*, claws of postabdomen and posterior tail spine; (J) *Bythotrephes arcticus*, claws of postabdomen and posterior tail spine; (K) *Bythotrephes transcaucasicus*, claws of postabdomen and posterior tail spine.

Onychopoda: Podonidae: Cornigerius: Species

1 Head with large dorsal outgrowth, bearing prominences of different size 2

1′ Head rounded with no dorsal outgrowth or with small outgrowth, bearing two short straight or slightly bent horns; postabdominal claws comparatively small, slightly diverging (Figs. 16.2.48 C–E) ..... *Cornigerius bicornis* (Zernov, 1901) [Ponto-Caspian. Invasive elsewhere]

2(1) Head with large dorsal outgrowth, bearing two long unguiform horns; postabdominal claws long, bent and strongly diverging (Figs. 16.2.48 F, G) ..... *Cornigerius maeoticus* (Pengo, 1879) [Ponto–Caspian. Invasive elsewhere]

2′ Head with large dorsal outgrowth, bearing two small prominences; postabdominal claws almost straight and slightly diverging (Figs. 16.2.48 H–J) ..... *Cornigerius lacustris* (Spandl, 1923) [Turkey: Lake Geljik]

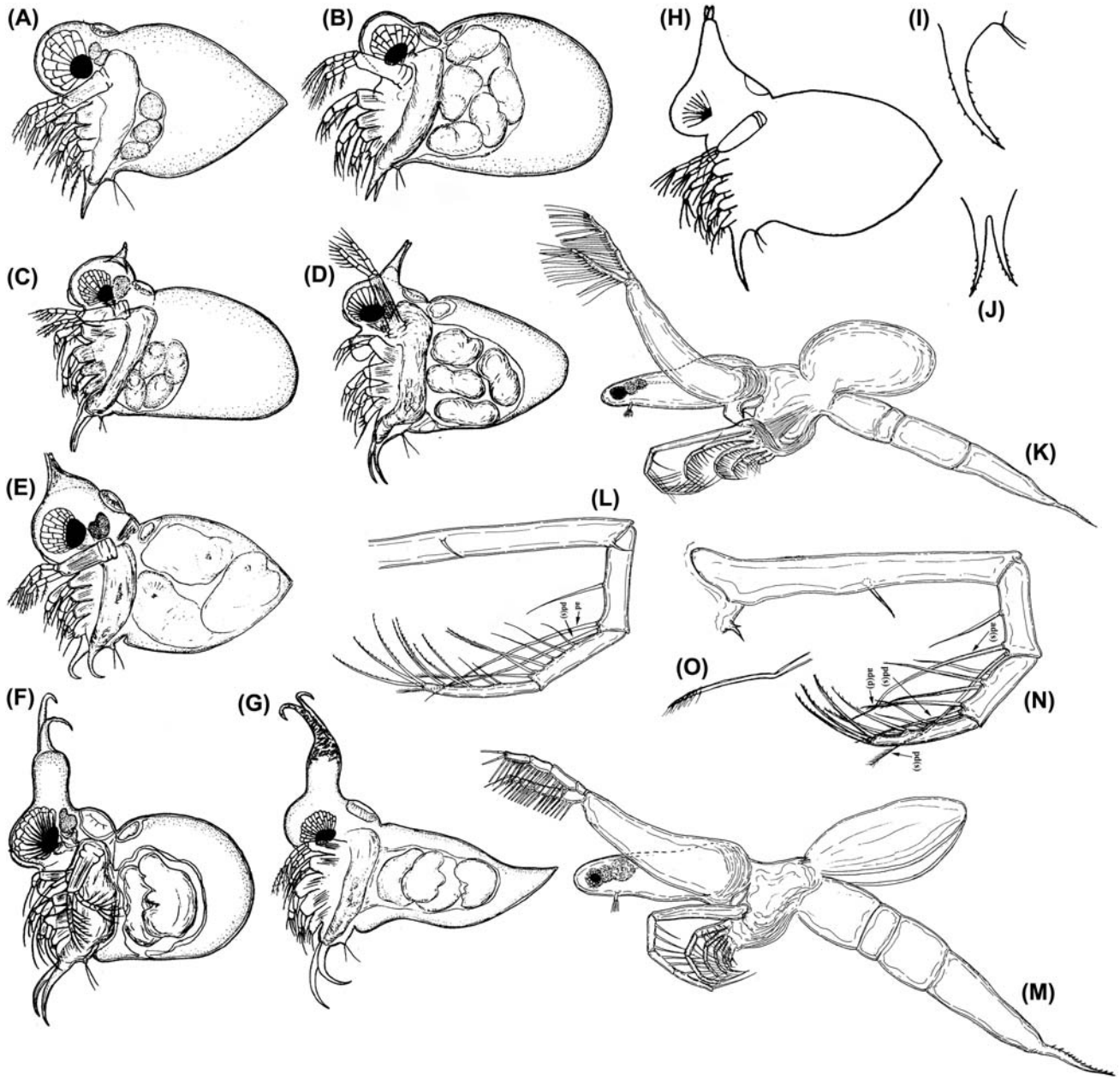


FIGURE 16.2.48 Representatives of Onychopoda (A–J) and Haplopoda (K–O): (A–B) *Podonevadne trigona*; (C–E) *Cornigerius bicornis*; (F–G) *Cornigerius maeoticus*; (H–J) *Cornigerius lacustris*; (K–L) *Leptodora kindtii*, general view and limb I; (M–O) *Leptodora richardi*; general view, limb I and, anterior distal seta of second segment of limb I.

Cladocera: Haplopoda: Leptodoridae: Leptodora: Species

1 Body size of adult females 5.0–21.0 mm; head 25.3%–33.6% body length; abdomen 30.3%–39.7% body length; limb I, second article with anterior distal seta glaborous (Figs. 16.2.48 J, K, L) ..... *Leptodora kindtii* (Focke, 1844) [Holarctic. Possible species complex]

1′ Body size of adult females 2.6–6.1 mm; head 30.9%–35.3% body length; abdomen 29.4%–34.3% body length; limb I, second article with anterior distal seta with fine setules distally (Figs. 16.2.48 M–O) ..... *Leptodora richardi* Korovchinsky, 2009 [China, Eastern Russia, Japan]

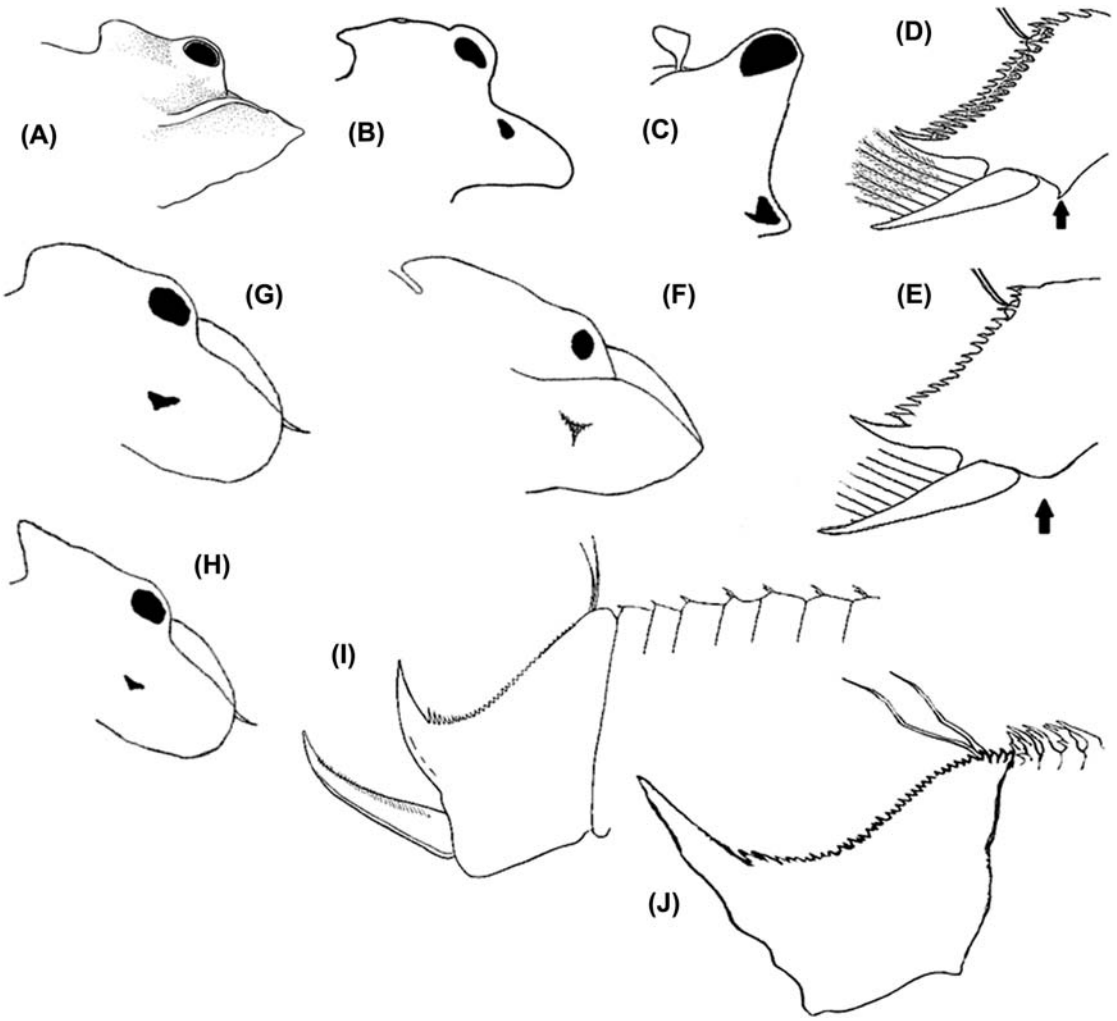


FIGURE 16.2.49 (A) *Eocyzicus* sp., head, lateral view; (B) *Imnadia yeyetta*, head, lateral view; (C) *Eulimnadia* sp., head, lateral view; (D) *Eulimnadia* sp., telson, lateral view; (E) *Limnadia lenticularis*, telson, lateral view; (F) *Cyzicus altus*, head, lateral view; (G) *Eoleptestheria* sp., lhead, lateral view; (H) *Leptestheria*, head, lateral view; (I) *Leptestheria*, telson and dorsal portion of abdomen, lateral view; (J) *Maghrebestheria maroccana*, telson and dorsal portion of abdomen, lateral view.

Branchiopoda: Diplostraca: Spinicaudata: Families

1	Fornicies extend to rostrum (Fig. 16.2.49 A)	2
1′	Fornicies do not extend to rostrum (Figs. 16.2.49 B)	**Limnadiidae**
2(1)	Rostrum lacking an apical spine [This family is in need of revision]	**Cyzicidae**
2′	Rostrum with a single apical spine (may be broken off, look for scar) [This family is in need of revision]	**Leptestheriidae**

Branchiopoda: Diplostraca: Spinicaudata: Limnadiidae: Genera

Adapted from Rogers et al. (2012).

1	Frontal organ pedunculate (Figs. 16.2.49 C)	2
1′	Frontal organ sessile (Fig. 16.2.49 B) [Europe]	*Imnadia yeyetta* Hertzog, 1935
2(1)	Telson without a ventral spiniform projection (Fig. 16.2.49 E) [Holarctic]	*Limnadia lenticularis* (L., 1761)

2′ Telson with a ventral spiniform projection (Fig. 16.2.49 D) ..... *Eulimnadia*
[Cosmopolitan, except Antarctica and Europe; species are defined by egg morphology (Belk, 1989; Rabet, 2010; Rogers et al., 2012), but in many the egg morphology is either unknown or incompletely known. For African species, see Rabet et al. (2015)]

Branchiopoda: Diplostraca: Spinicaudata: Cyzicidae: Genera

1 Head with dorsoposterior deep cleft just anterad of carapace point of attachment (Fig. 16.2.49 F) ..... *Cyzicus*
[Widely distributed, genus in need of revision]

1′ Head lacking a dorsoposterior deep cleft (Fig. 16.2.49 A) ..... *Eocyzicus*
[Widely distributed, genus in need of revision]

Branchiopoda: Diplostraca: Spinicaudata: Leptestheriidae: Genera

Adapted from Thiéry (1988).

1 Occiput acute (Figs. 16.2.49 H) 2

1′ Occiput rounded (Fig. 16.2.49 G) ..... *Eoleptestheria*
[Widely distributed, genus in need of revision]

2(1) Posterior somites with dorsal spines simple, small or absent (Figs. 16.2.49 I) ..... *Leptestheria*
[Widely distributed, genus in need of revision]

2′ Posterior somites with dorsal spines large and bearing smaller spines on posterior surface (Fig. 16.2.49 J) .... *Maghrebestheria maroccana* Thiéry, 1988
[Morocco]

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Chapter 16.3

Arthropoda: Ostracoda

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INTRODUCTION

Nonmarine ostracods are small, benthonic or nekto-benthonic crustaceans with a calcified bivalved carapace, mostly 0.4–2.0 mm long in the adult stage but with some smaller interstitial taxa and a few temporary pond taxa up to 8.0 mm; the Palaearctic genera range from 0.2 mm (e.g., *Nannokliella*) to around 5.0 mm (e.g., *Hungarocypris*). They typically have nine instars consisting of eight juvenile and one adult stage (postmaturation molting is virtually unknown), although the Entocytheridae have only eight instars. All extant nonmarine Ostracoda belong to the superfamilies Cypridoidea, Darwinuloidea, or Cytheroidea, within the order Podocopida of the subclass Podocopa. Nonmarine ostracods are found throughout the Palaearctic in most aquatic environments including freshwater and saline lakes, streams and rivers, springs, wetlands, temporary ponds, and groundwater; they are sometimes even found in

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(semi-) terrestrial habitats. The great majority of nonmarine genera are free living, typically benthonic (all Cytheroidea and Darwinuloidea), crawling and burrowing in sediments or climbing on aquatic plants, although many members of the Cypridoidea (excluding the Candoninae) can swim and are best regarded as nekto-benthonic. The exception is the Entocytheridae, which are commensal on larger crustaceans such as crayfish. Over 700 freshwater ostracod species have been described in the Palaearctic region, more than twice as many as in the Nearctic (Martens et al., 2008).

LIMITATIONS

These keys to podocopid ostracod superfamilies, families, and genera use morphological characteristics of the carapace and appendages of adult female specimens. Adult males are common in some taxa, but rare or completely unknown in others (e.g., Smith et al., 2006). Some species show geographical parthenogenesis, for example, European sexual populations of the cypridoidean *Eucypris virens* and the cytheroidean *Limnocythere inopinata* are restricted to circum-Mediterranean areas, whereas female only, parthenogenetic populations are much more widely distributed (Horne et al., 1998; Horne & Martens, 1999; Schmit et al., 2013). Although the keys may also work for adult males (if found) of many taxa, it is advisable to be aware that sexual dimorphism (in some appendages as well as in carapace shape) may mislead (e.g., Fig. 16.3.27 O–P).

Juvenile specimens have fewer pairs of appendages (depending on growth stage), and their carapaces are typically more posteriorly tapered than those of adults, as well as lacking such well-developed calcified inner lamellae. The unwary may also be confused by the phenotypic variation in the development of spines, hollow tubercles, or solid nodes on the carapaces of some taxa (e.g., Figs. 16.3.27 M–P). Where possible, we have used characters that can be determined without the need for full dissections.

We have not attempted to provide keys to species level because many taxa need revision and there are likely to be many as yet undiscovered species, particularly in regions that have so far received little attention from ostracod specialists. Those who wish to identify species will need to refer to specialist publications. As an excellent starting point for studies of Palaearctic freshwater ostracods, Meisch's (2000) monograph provides keys and illustrations for more than 150 species from western and central Europe. Karanovic's (2012) *Recent Freshwater Ostracods of the World* includes keys to genera and species. Martens & Savatenalinton's (2011) comprehensive checklist of free-living freshwater ostracods of the world provides a good introduction to the specialist literature and lists Palaearctic species.

The drawings of carapaces and appendages (Figs. 16.3.1–26) are all originals drafted specially for this chapter, based on published illustrations or our own specimens of typical species, with the aim of showing key characteristics of the genera. As such they are best regarded as cartoons to aid the use of the keys and are not intended to be used for species-level identification. Therefore, we have deliberately not indicated which species they represent.

TERMINOLOGY AND MORPHOLOGY

Two spellings of the informal name for the Ostracoda are in common use: ostracode and ostracod; in this chapter, we use the latter. The essential anatomy and terminology of appendages of the three freshwater superfamilies, Darwinuloidea, Cypridoidea, and Cytheroidea, are shown in Figs. 16.3.1–3, respectively. Additional key details of appendage and carapace morphology are illustrated and labeled in Figs. 16.3.4–26, and finally some scanning electron microscope (SEM) images of ostracod shells together with colour images (from high resolution video microscopy) of living specimens are shown in Fig. 16.3.27. Arrows on the figures indicate the anterior direction. A general introduction to the morphology of freshwater ostracod carapaces and appendages can be found in Smith et al. (2015).

The following are abbreviations used in our keys:

CIL Calcified inner lamella
LV Left valve
RV Right valve
AMS Adductor muscle scars
A1 Antennula
A2 Antenna
Md Mandibula
Mx1 Maxillula (first maxilla)
L5 Fifth limb (first thoracic leg/second maxilla/maxilliped)
L6 Sixth limb
L7 Seventh limb
UR Uropodal ramus
PA Post-abdomen

MATERIAL PREPARATION AND PRESERVATION

Field collection techniques for freshwater ostracods are described by Martens and Horne (2016); further details can

be found in Scharf et al. (2014) and Smith et al. (2015). If a net has been used for collecting then further sieving may not be necessary, but samples may be washed through sieves with a gentle jet of water to concentrate the size fraction that includes ostracods. A mesh size of 0.25 mm will retain adults of most species but not small juveniles, while a 125μm mesh will retain most identifiable juveniles; a large-mesh sieve can be used above the finer sieve to remove stones and plant material. Specimens can be picked out with a pipette under a low-power stereo microscope from small amounts of sample spread in water on a tray or a petri dish. Doing this within a few hours of collection can make it easy to see and catch living, moving ostracods, but the same technique can be applied to preserved material. Specimens can be also picked from dry sieved residues scattered on a tray using a wetted artist's fine paintbrush (forceps or tweezers are not recommended as shells may easily be broken). It is worth bearing in mind that samples may contain empty carapaces and separated valves that constitute a time-averaged assemblage of identifiable shells and thus may include representatives of additional taxa that inhabit the waterbody but were not found as living specimens on that particular occasion of sampling. Ethanol is recommended for fixing and preserving ostracods caught alive with appendages intact. Initial treatment with 10–30% ethanol helps to ensure that the valves are preserved in an open, gaping condition, which makes subsequent separation for dissection purposes much easier. If live ostracods are placed immediately in more concentrated ethanol they tend to close their shells tightly and they can be difficult to open subsequently for study; Scharf et al. (2016) explain methods for opening closed ostracod carapaces. For long-term preservation 70% ethanol is recommended. If specimens are required for DNA analysis, preservation in 95–99% pure ethanol is necessary. Specimens can be preserved in ethanol on small sealable containers; alternatively they can be dried and mounted on standard micropaleontological slides, an option that is also useful for empty ostracod shells. Shells intended for geochemical analyses are best stored dry and loose on micropaleontological slides or in small sealable containers; fossil shell assemblages can be sorted (e.g. into species, adults, and juveniles) and mounted on micropalaeontological slides using water-soluble glue (so that they can be moved again if necessary). A microscope with higher magnifications (at least to 100× and ideally with phase contrast) is generally necessary for examining the morphology of dissected appendages. The general morphology of shells (whether dry or wet) can be examined in incident light, in which case staining with a dark water soluble dye (such as food coloring) may be helpful in revealing fine details of surface ornament or hinge structure. Features such as adductor muscle scars and marginal pore canals are more easily seen in transmitted light, preferably with specimens immersed in water, ethanol or glycerine for clearer views.

Full or partial dissections of appendages can be carried out under a stereo microscope at 20x to 50x magnification in combined incident and transmitted light, ideally using specimens preserved in ethanol (dry specimens can be soaked in water or ethanol and dissected, but trapped air bubbles can be problematic). A specimen can be placed in a drop of water or ethanol on a glass slide to begin dissection. Using a pair of fine needles (e.g. entomological pins mounted in pin chucks), carapaces can be opened, the valves being separated and removed to be preserved separately (e.g. dry on a micropaleontological slide); a drop of a suitable mounting medium (e.g. Glycerine or Hydro-Matrix; PolyVinyl Lactophenol is no longer recommended, due to its carcinogenic properties) is placed over the body before appendages are teased apart and arranged on the slide, the dissection finally being protected by the addition of a glass cover slip. Valves can be left on the same slide as the appendages but may be broken when the cover slip is added. Dissection takes patience and practice; it is best to start with relatively large specimens if such are available. Partial dissections or simple "squash" mounts in which the appendages are left attached to the body are easier and can still be useful. After a few days it is a good idea to seal the edges of the cover slip with nail varnish to prevent gradual drying of the mounting medium and invasion of the dissection by air bubbles if Glycerine is used. Namiotko et al. (2011) provide an excellent illustrated guide to dissection techniques.

ACKNOWLEDGMENTS

We thank the editors, Christopher Rogers and James Thorp, for their advice, their encouragement, and above all their patience during the writing of this chapter.

KEYS TO OSTRACODA

These keys use adult female characters of freshwater ostracods in the class Podocopa, order Podocopida.

Ostracoda: Superfamilies

1	AMS pattern not a circular to ovate rosette; valves with CIL narrow or wide, body with 1−3 pairs of walking legs 2
1′	AMS pattern a distinct circular or ovate rosette; carapace with CIL very narrow; body with two pairs of walking legs (L6 & L7) (Fig. 16.3.1) ..... Darwinuloidea, one family: **Darwinulidae**
2(1)	AMS pattern a cluster arranged like a "pawprint," with scars tightly clustered or more openly arranged; carapace usually with a moderately wide CIL; body with one pair of walking legs (L6); L7 an inverted cleaning limb (Fig. 16.3.2) ..... **Cypridoidea**
2′	AMS pattern a vertically stacked arrangement of four scars (some occasionally subdivided in two); carapace with moderately wide CIL; body with three pairs of walking legs (L5, L6, & L7) (Fig.16.3.3) ..... **Cytheroidea**

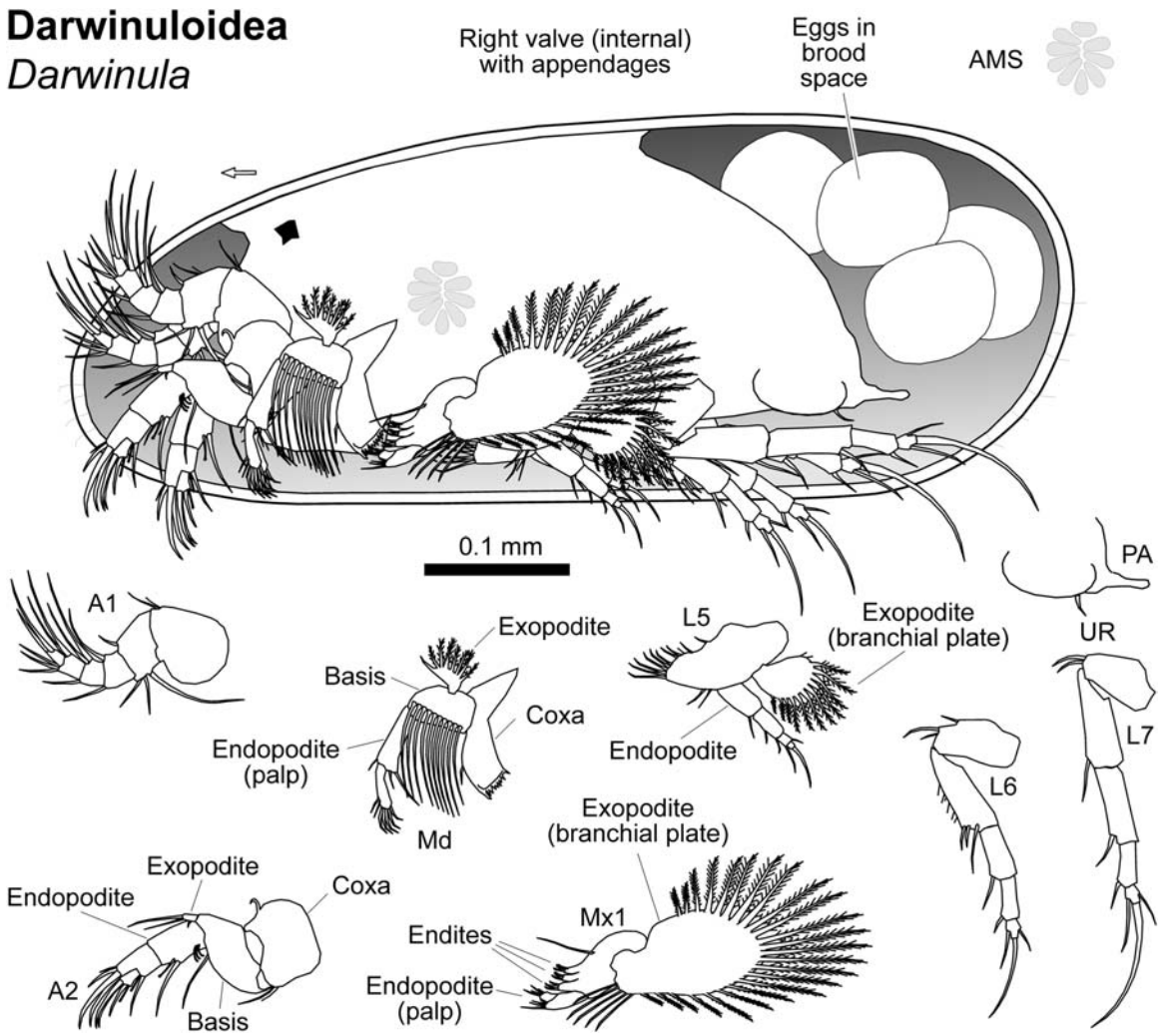


FIGURE 16.3.1 General anatomy of a typical darwinuloidean ostracod (adult female).

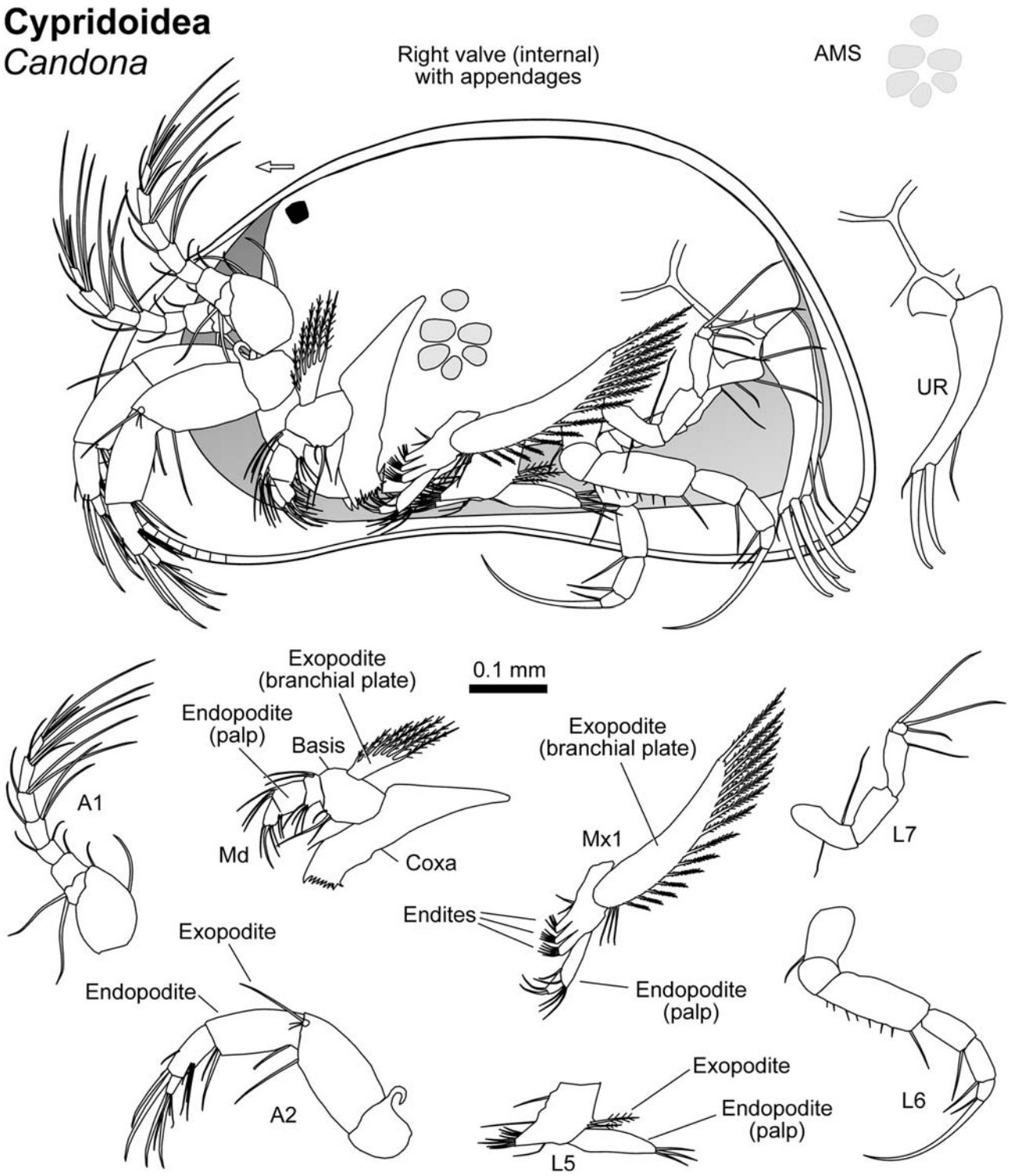


FIGURE 16.3.2 General anatomy of a typical cypridoidean ostracod (adult female).

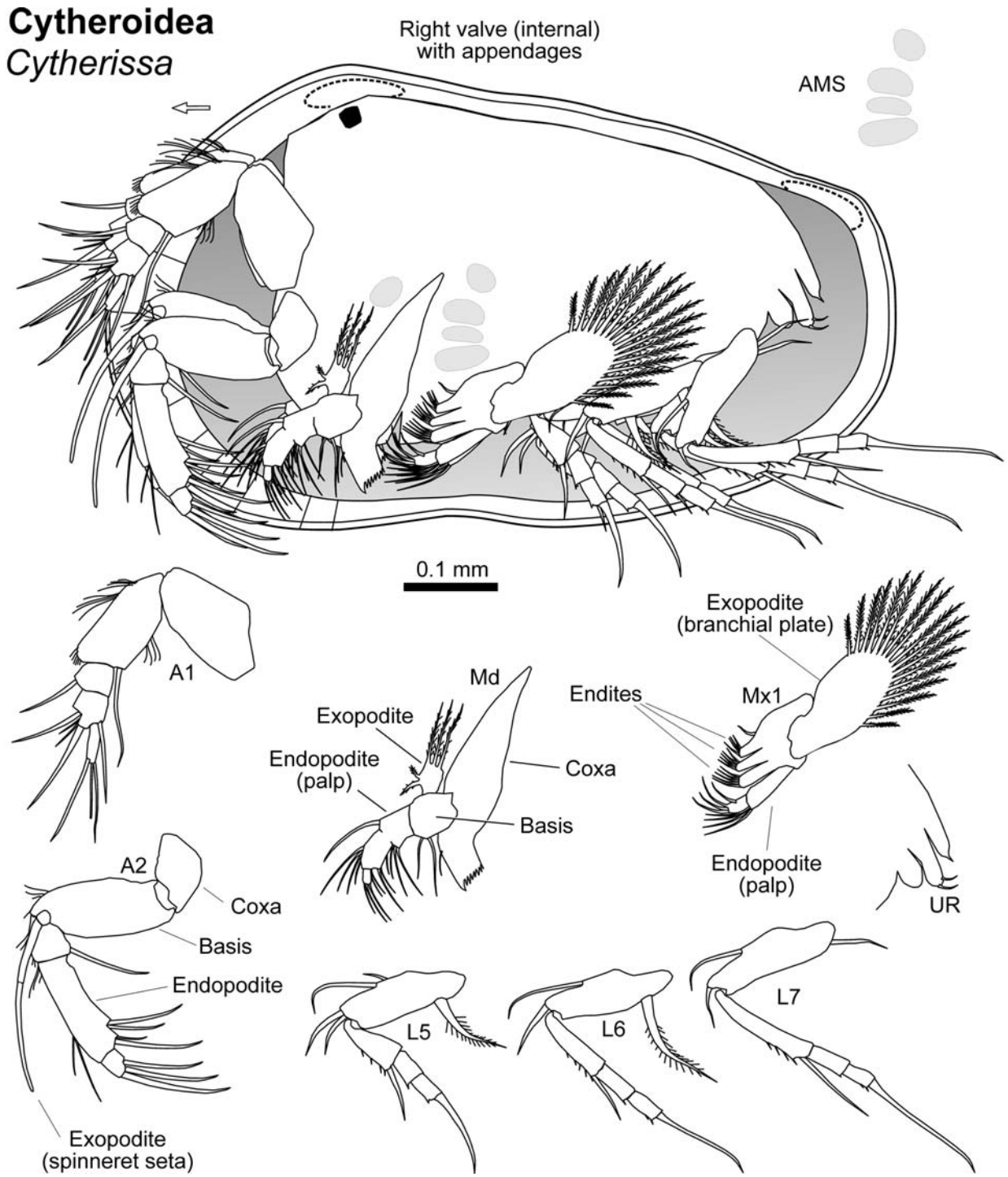


FIGURE 16.3.3 General anatomy of a typical cytheroidean ostracod (adult female).

Ostracoda: Darwinuloidea: Darwinulidae: Genera

Darwinulids are benthonic, infaunal or interstitial, nonswimming ostracods, found in most aquatic settings (and some terrestrial habitats), sometimes in abundance. Six extant darwinulid genera are known, four of which occur in the Palaearctic (*Darwinula, Microdarwinula*, *Penthesilenula*, and *Vestalenula*). The genera *Alicenula* (Neotropical −Afrotropical − Oriental) and *Isabenula* (Oriental) have not yet been identified living in the Palaearctic.

The carapace is small (0.4−0.8 mm length), smooth, white, thinly calcified, CIL very narrow, with vestibules absent, and a distinctive rosette-shaped AMS pattern. Valve overlap may be LV>RV or RV>LV. The larger valve may have internal teeth in anteroventral, posteroventral, or posterior positions, which function as "stop-ridges" against which the free margin of the smaller valve rests when the carapace is closed. A posteroventral external keel with a similar function may be present in the smaller valve. The normal pores are simple, and a median eye is present. The A1 has six articulated podomeres. Whereas the A2 endopodite has three articulated podomeres, without swimming setae; the exopodite is a reduced podomere with two long and one very short setae. The Md palp has a row of eight rake-like setae and a small branchial plate with up to eight rays. Mx1 has a large branchial plate with four reflexed, forward-pointing rays. L5 is a maxilliped with a small branchial plate and a leg-like palp comprising three endopodite podomeres. L6 and L7 are both walking legs similar in structure and direction. Uropodal ramus (UR) is reduced to a seta or is lacking and is situated anteriorly to an elongate post-abdomen (PA). Ovaries do not originate within a duplicature. Females carry eggs or early stage juveniles in a posterior brood space of the carapace and are usually visible through shell. Males are exceptionally rare, known only in one species.

1	Smaller valve without posteroventral external keel	2
1′	Smaller valve (RV) with posteroventral external keel (Figs. 16.3.4 D, E)	*Vestalenula*
2(1)	Larger valve with at least one internal tooth; LV>RV	3
2′	Larger valve without internal teeth; RV>LV (Figs. 16.3.1 and 16.3.4 A)	*Darwinula*
3(2)	AMS situated at approximately mid-length; valves in lateral view ovate (Fig. 16.3.4 C)	*Microdarwinula*
3′	AMS situated well in front of mid-length; valves in lateral view elongate (Fig. 16.3.4 B)	*Penthesilenula*

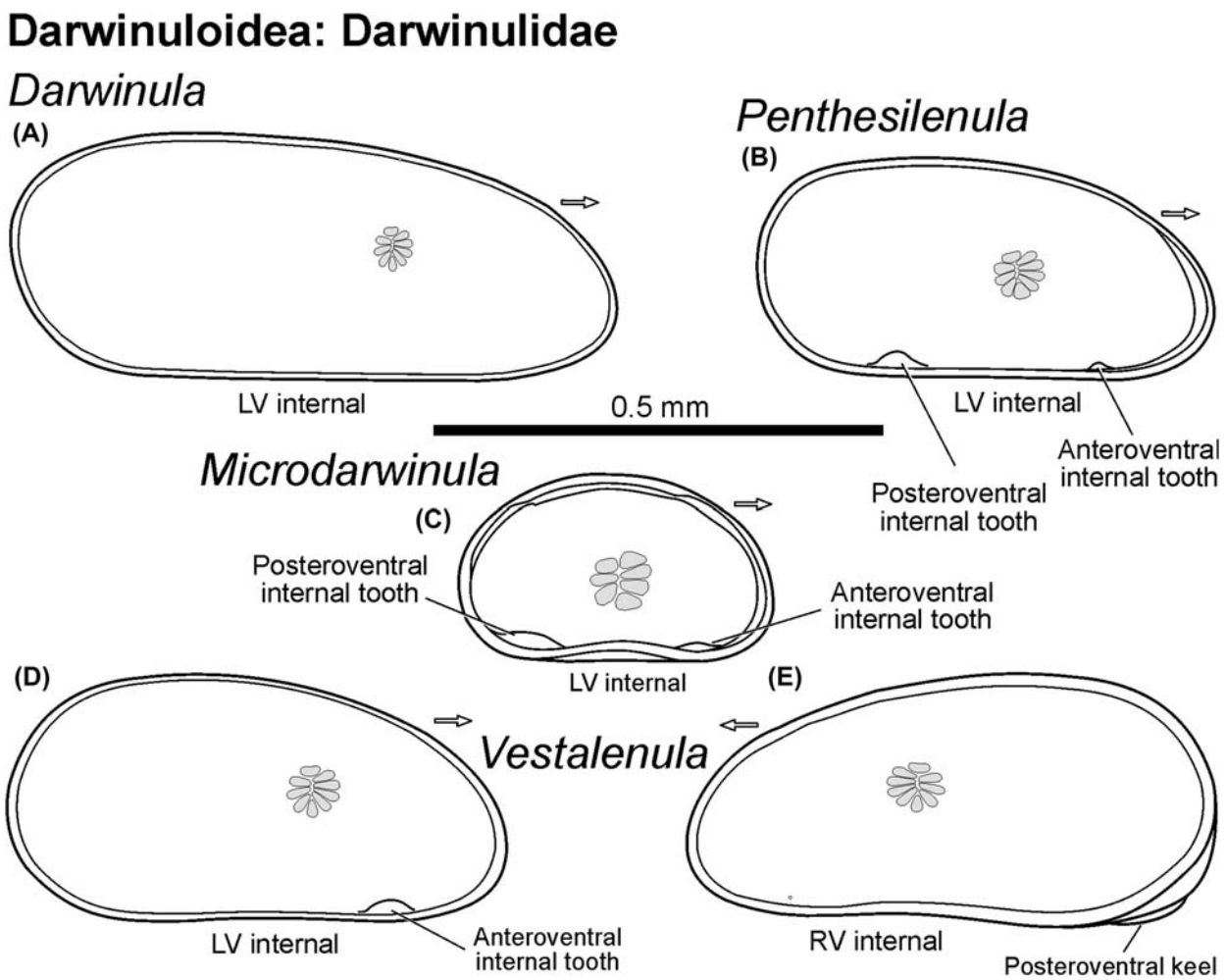


FIGURE 16.3.4 Key characteristics of genera of the Darwinulidae.

Ostracoda: Cypridoidea: Families

The superfamily Cypridoidea contains the majority of living nonmarine species, many of which are active nekto-benthonic swimmers with well-developed long swimming setae on the first and second antennae (A1 and A2). In crawlers and burrowers, these setae are reduced or absent and such animals live infaunally, interstitially, or as part of the epibenthos, for example, members of the Candoninae. Four families are represented in the Palaearctic: the Ilyocyprididae, Notodromadidae, Cyprididae, and Candonidae.

The carapace surface is usually smooth or finely ornamented, and the dorsal margin has weak or simple hinge teeth. Carapace size and shape are variable, with strong sexual dimorphism in some genera. CIL is usually well developed. The basic AMS pattern is a "pawprint" with three to four scars in an arcuate row in front of two scars in a vertical row. Normal pores are simple. Lateral ocelli of median eye sometimes feature corresponding eyespots developed in the valves. A1 has six to eight podomeres. A2 endopodite has three or four podomeres, with the exopodite reduced to a small scaliform protuberance bearing at most three setae. Md palp has a small branchial plate with up to six rays. Mx1 has a large branchial plate with up to three reflexed, forward-pointing rays. L5 usually features a small branchial plate, sometimes reduced to one or two setae; the endopodite has one or two podomeres, forming a small palp in the female but enlarged to form a clasper in the male. L6 is a walking leg with a strong terminal claw. L7 is bent dorsally as a cleaning leg, usually with three terminal setae; the small terminal podomere may be modified as a pincer. UR typically is well developed with terminal claws but may be reduced to a flagellum. The gonads are located within the duplicature of the valves. In the male, a portion of the vas deferens is modified to form an ejaculatory duct, the Zenker's organ, separate from the copulatory appendage (hemipenis), which can be large. Females never have a brood chamber.

Ilyocyprids may be confused with limnocytherines (superfamily Cytheroidea), which also have long, straight hinges and dorsomedian sulci; they are easily separated by looking at the AMS, and furthermore many limnocytherids have laterally compressed, flattened areas near the anterior and posteroventral margins of the valves, never seen in ilyocyprids. Although the vast majority of Cyprididae have an L5 with one endopodite podomere, there are a few exceptions in which there are two. The position of the frontal and mandibular scars, which are always anterior to the AMS, is helpful in determining orientation. Some Cyprididae (e.g. Cypridopsinae) have quite tightly clustered, rounded AMS but without the separation of the uppermost one seen in the Candonidae.

1	Valves without dorsomedian sulci and with short straight (less than two-thirds the length of the carapace) or arched hinge lines; L5 endopodite with one podomere, L7 with a terminal pincer or with simple terminal setae 2
1′	Valves subrectangular with two dorsomedian sulci and a long, fairly straight dorsal hinge line, more than three-quarters of the length; L5 endopodite with two podomeres, L7 with simple terminal setae (Fig. 16.3.5) ..... Ilyocyprididae, one genus: *Ilyocypris*
2(1)	Carapace ovoid, elongate ovoid or reniform, ventral margin in lateral view convex or sinuous, rarely straight; valve margins without an external flange; A2 swimming setae well developed, reduced, or absent 3
2′	Carapace ovoid with a straight ventral margin in lateral view; valve margins rimmed with a flat external flange, widest anteriorly; A2 with well-developed swimming setae (Fig. 16.3.6) ..... **Notodromadidae**

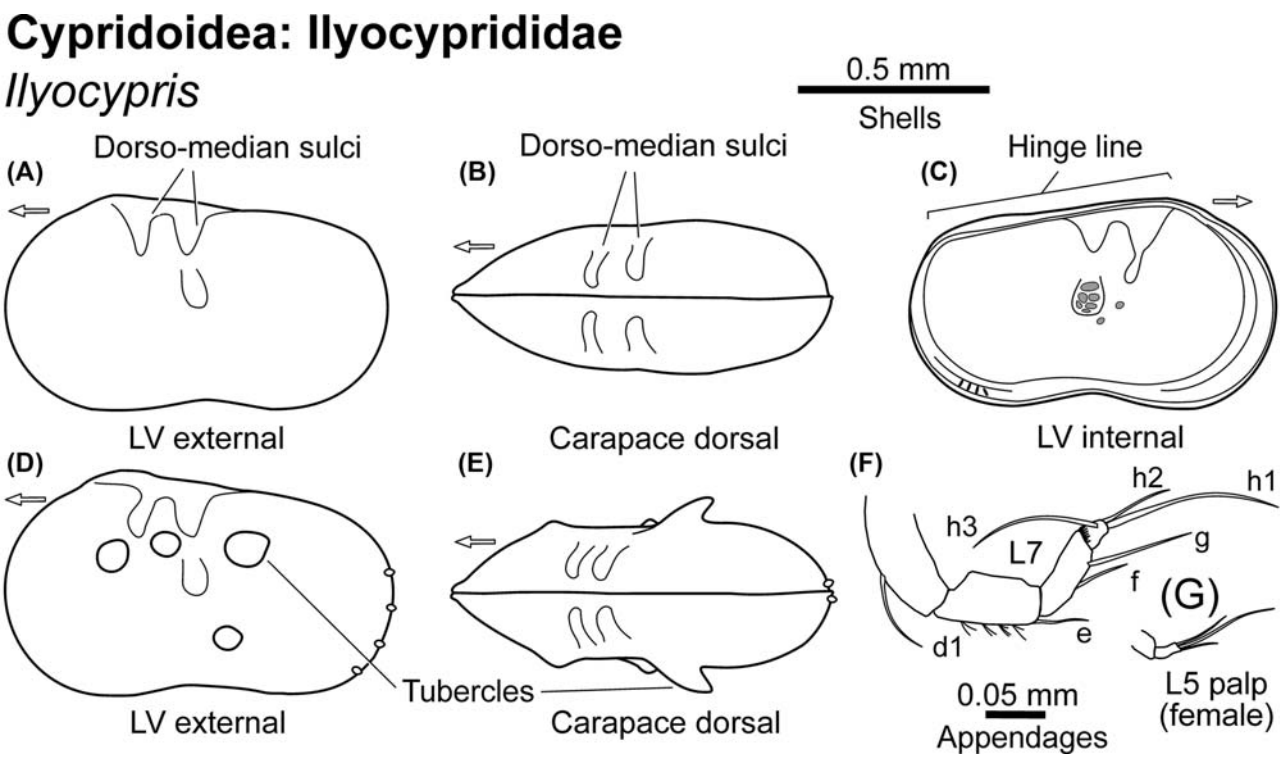


FIGURE 16.3.5 Key characteristics of the Ilyocyprididae, genus *Ilyocypris*.

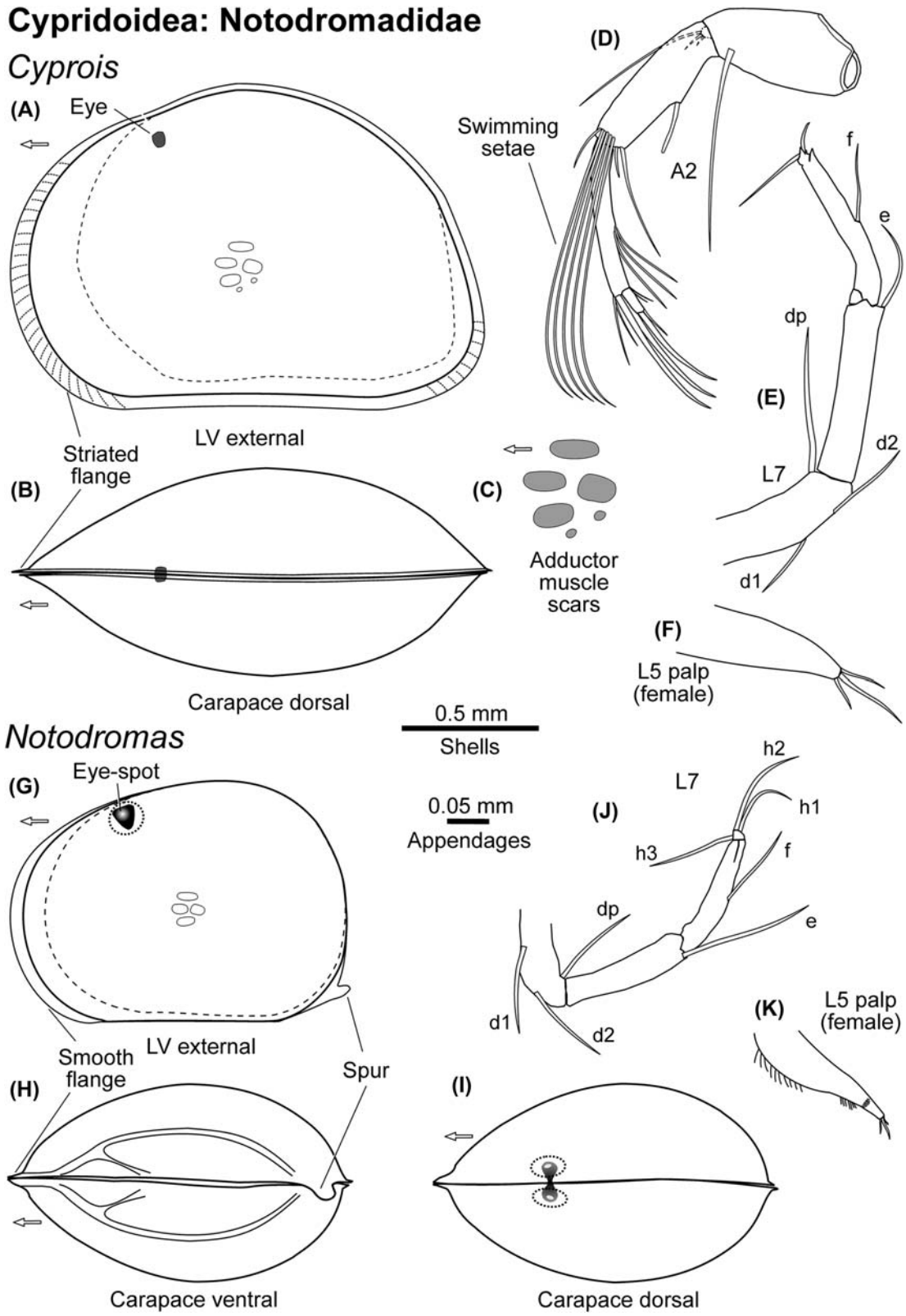


FIGURE 16.3.6 Key characteristics of genera of the Notodromadidae.

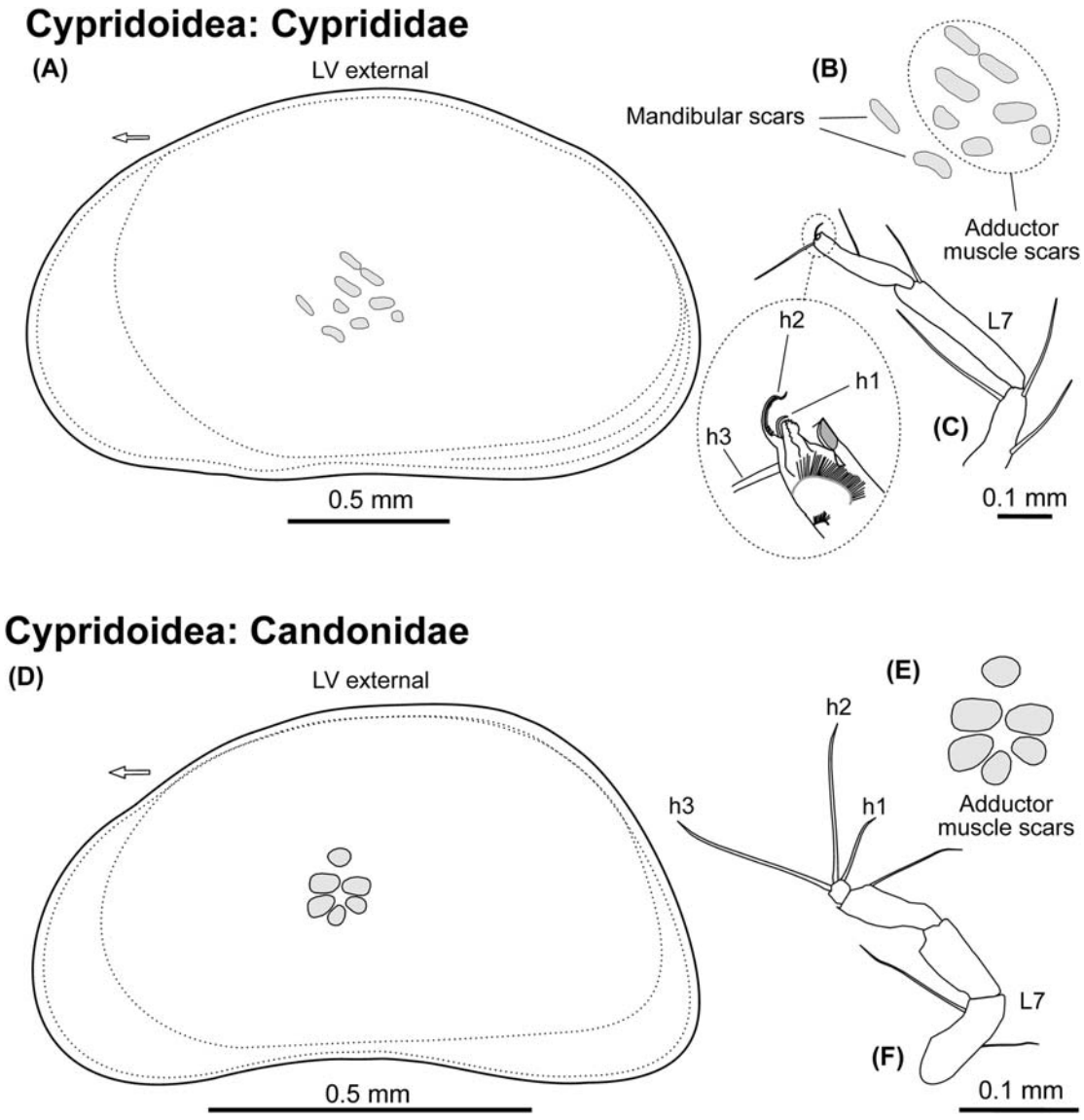


FIGURE 16.3.7 Key characteristics of the Cyprididae and Candonidae.

3(2) AMS a "pawprint" of rounded, often elongate, and sometimes subdivided scars; carapace typically with maximum height close to or well in front of midpoint; L7 with a terminal pincer (Figs. 16.3.7 A–C) ..... **Cyprididae**

3′ AMS a tight "pawprint" cluster of rounded wedge-shaped scars, the uppermost is slightly separated from the rest in some genera; carapace typically with maximum height close to or well behind midpoint; L7 without terminal pincer (Figs. 16.3.7 D–F) ..... **Candonidae**

Ostracoda: Cypridoidea: Notodromadidae: Genera

1 Valves with prominent striated marginal flanges; carapace compressed in dorsal/ventral view; cleaning leg (L7) with a terminal pincer; eye central with ocelli fused (Figs. 16.3.6 A–D) ..... *Cyprois*

1′ Valve flanges not striated; carapace inflated in dorsal/ventral view, with a flattened ventral area rimmed with ridges; cleaning leg (L7) without a terminal pincer; eye with lateral ocelli separate and corresponding to an eyespot in each valve (Figs. 16.3.6 E–I) .... *Notodromas*

Ostracoda: Cypridoidea: Cyprididae: Subfamilies and Genera

Care must be taken not to confuse marginal septa (internal walls between the inner and outer lamellae) with marginal pore canals (internal tubes that open externally on the outer margin and bear sensilla); both features must be viewed in transmitted light.

1	UR well developed with terminal claws 2
1′	UR (if present) reduced, flagelliform and without terminal claws, or absent (Fig. 16.3.8) ..... **Cypridopsinae**
2(1)	Endoskeletal UR attachment strut without a Triebel's Loop 3
2′	Endoskeletal UR attachment strut with a Triebel's Loop (Fig. 16.3.18) ..... **Cypricercinae**
3(2)	Endoskeletal UR attachment strut without a distal triangular reinforcement 4
3′	Endoskeletal UR attachment strut with a distal triangular reinforcement (Figs. 16.3.9 and 16.3.10) ..... **Herpetocypridinae**
4(3)	UR with one posterior seta 5
4′	UR with two posterior setae (Fig. 16.3.11) ..... Hungarocypridinae, one genus: *Hungarocypris*
5(4)	L6 with two terminal claws 6
5′	L6 with one terminal claw 8
6(5)	L6 h1-seta unguiform, more than half the length of the terminal claw (h2), h3-seta short 7
6′	L6 h3-seta long, unguiform, more than half the length of the terminal claw (h2), h1-seta short (Figs. 16.3.12 A–D) ..... Scottiinae, one genus: *Scottia*
7(6)	L5 palp with two podomeres (Figs. 16.3.12 E–H) ..... Limanocypridinae, one genus: *Limanocypris*
7′	L5 palp with one podomere (Figs. 16.3.12 I–K) ..... **Eucypridinae** (in part)
8(5)	A2 with swimming setae long, short, or reduced 9
8′	A2 swimming setae absent (Fig. 16.3.13 A) ..... Herpetocyprellinae, one genus: *Herpetocyprella*
9(8)	CIL present anteriorly and posteriorly 10
9′	CIL very broad anteriorly (with short radial marginal septa), absent posteriorly (Figs. 16.3.13 B–D) Isocypridinae, one genus: *Isocypris*
10(9)	Marginal zone without radial septa; carapace in dorsal view rounded or elongate 11
10′	Marginal zone with prominent radial anterior marginal septa; carapace in dorsal view rounded, globular (Fig. 16.3.14 A–B) ..... Cyprettinae, one genus: *Cypretta*
11(10)	Carapace ovoid or subtriangular in lateral view, moderately inflated in dorsal/ventral view; selvage peripheral or inwardly displaced in either or both valves 12
11′	Carapace markedly elongate in lateral and dorsal/ventral views; RV selvage peripheral, LV selvage inwardly displaced anteriorly and posteriorly (Figs. 16.3.14 C–F) ..... Dolerocypridinae, one genus: *Dolerocypris*
12(11)	Anterior selvage peripheral or inwardly displaced in one valve only 13
12′	Anterior selvage inwardly displaced in both valves ..... **Cypridinae**
13(12)	Free margin of one valve typically rimmed with small blunt spines (sometimes absent) ..... **Cyprinotinae**
13′	Free margins of both valves smooth or with small pointed marginal spines ..... **Eucypridinae** (in part)

Ostracoda: Cypridoidea: Cyprididae: Cypridopsinae: Genera

1	LV overlapping RV ventrally 2
1′	RV overlapping LV ventrally 4
2(1)	Posterior CIL in LV without a conspicuous inner list; A2 swimming setae well-developed or reduced 3
2′	Posterior CIL in LV with a conspicuous, oblique double inner list; A2 swimming setae well developed (Figs. 16.3.8 A–E) ..... *Cypridopsis*
3(2)	A2 swimming setae reduced; UR present (Figs. 16.3.8 F–H) ..... *Cavernocypris*
3′	A2 swimming setae well developed or reduced; UR absent (Fig. 16.3.8 I–J) ..... *Pseudocypridopsis*
4(1)	Mx1 palp terminal podomere elongate 5
4′	Mx1 palp terminal podomere spatulate; A2 swimming setae well developed or reduced (Figs. 16.3.8 K–M) ..... *Potamocypris*
5(4)	Mx1 outer endite with one smooth and one serrated bristle; A2 swimming setae well developed; UR with evenly tapering, triangular proximal part (Figs. 16.3.8 N–Q) ..... *Sarscypridopsis*
5′	Mx1 outer endite with two serrated bristles; A2 swimming setae well developed or reduced; UR proximal part cylindrical, narrowing abruptly to distal flagellum (Figs. 16.3.8 R–U) ..... *Plesiocypridopsis*

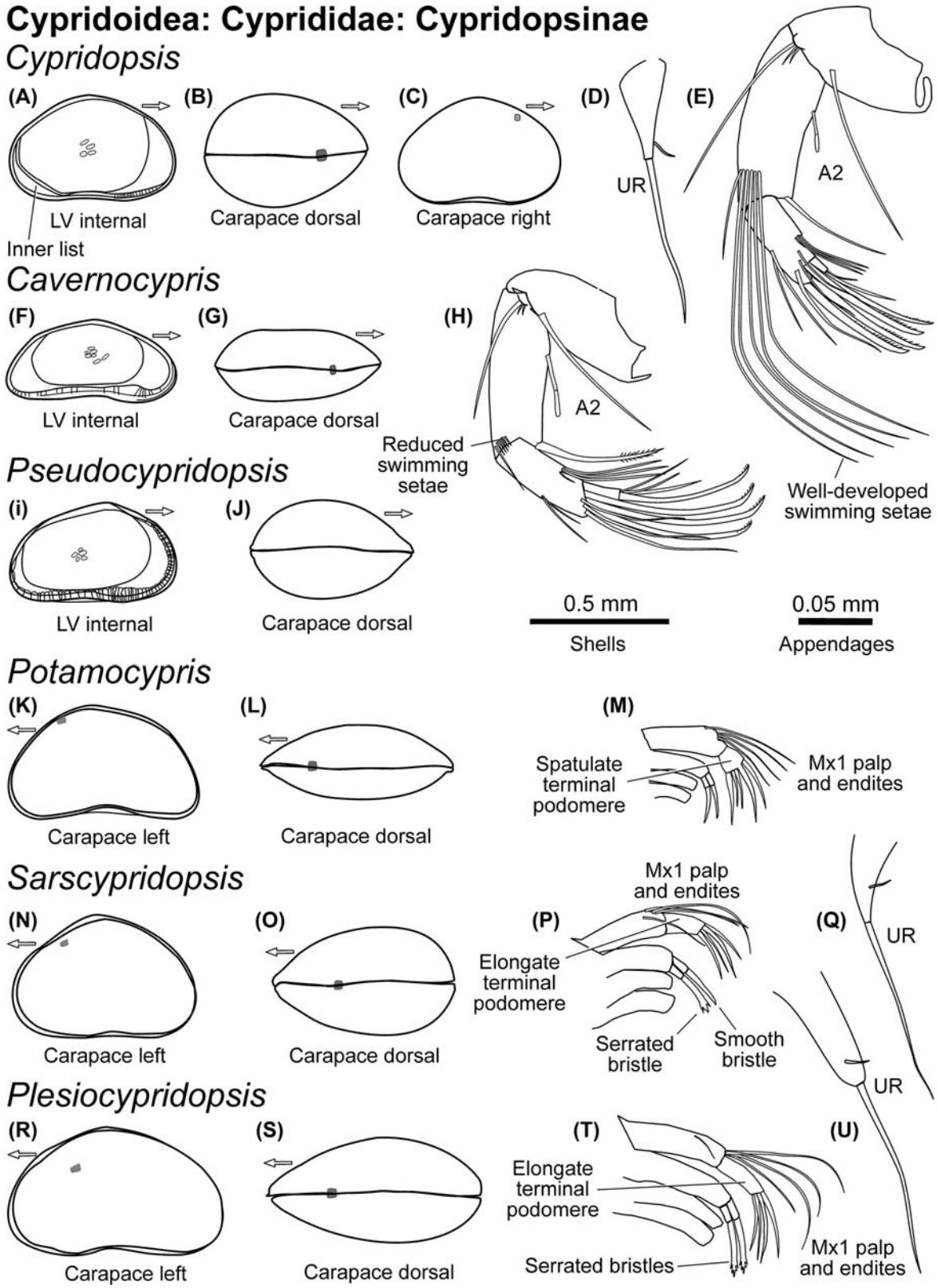


FIGURE 16.3.8 Key characteristics of genera of the Cyprididae, subfamily Cypridopsinae.

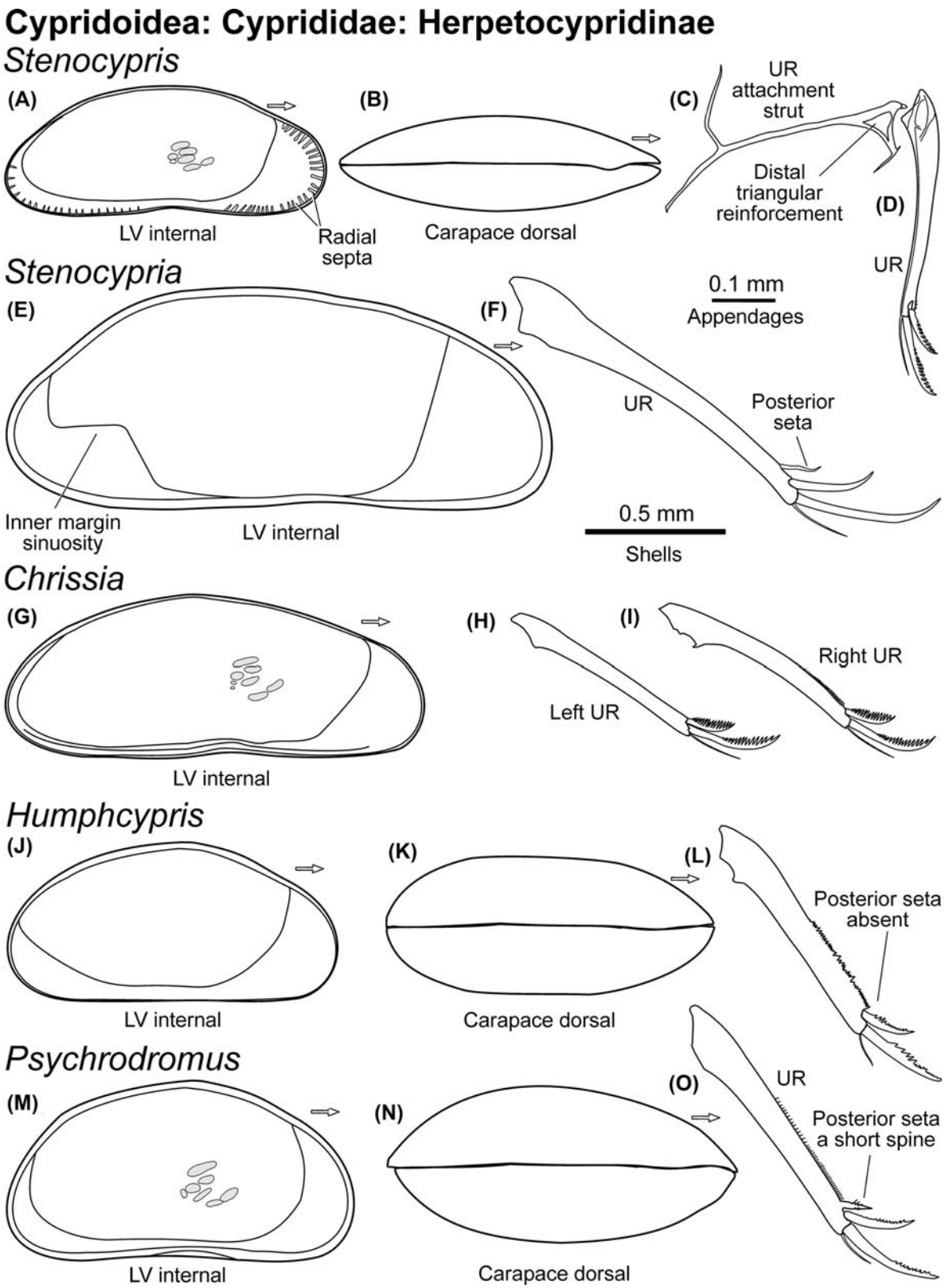


FIGURE 16.3.9 Key characteristics of genera of the Cyprididae, subfamily Herpetocypridinae.

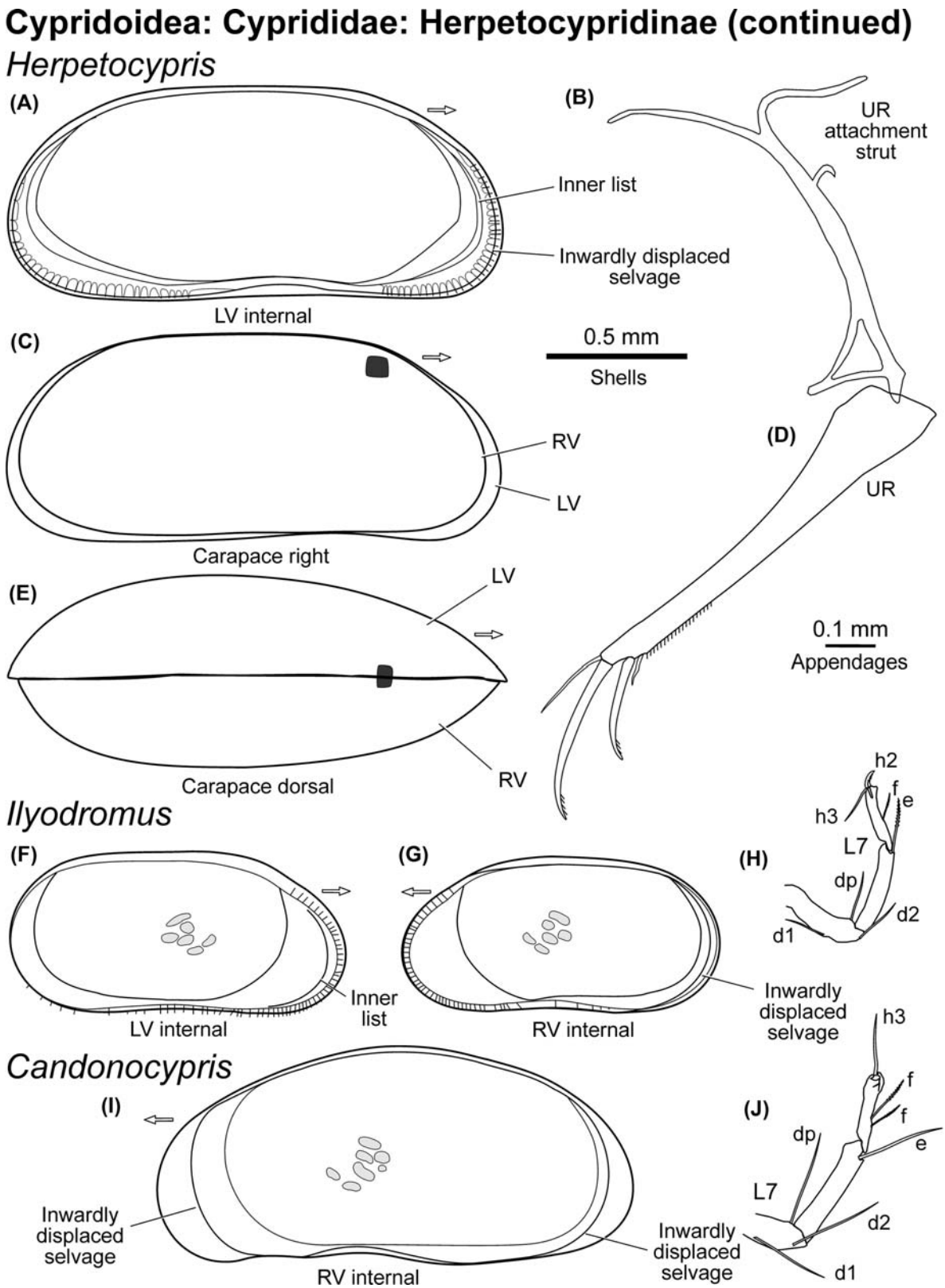


FIGURE 16.3.10 Key characteristics of genera of the Cyprididae, subfamily Herpetocypridinae (continued).

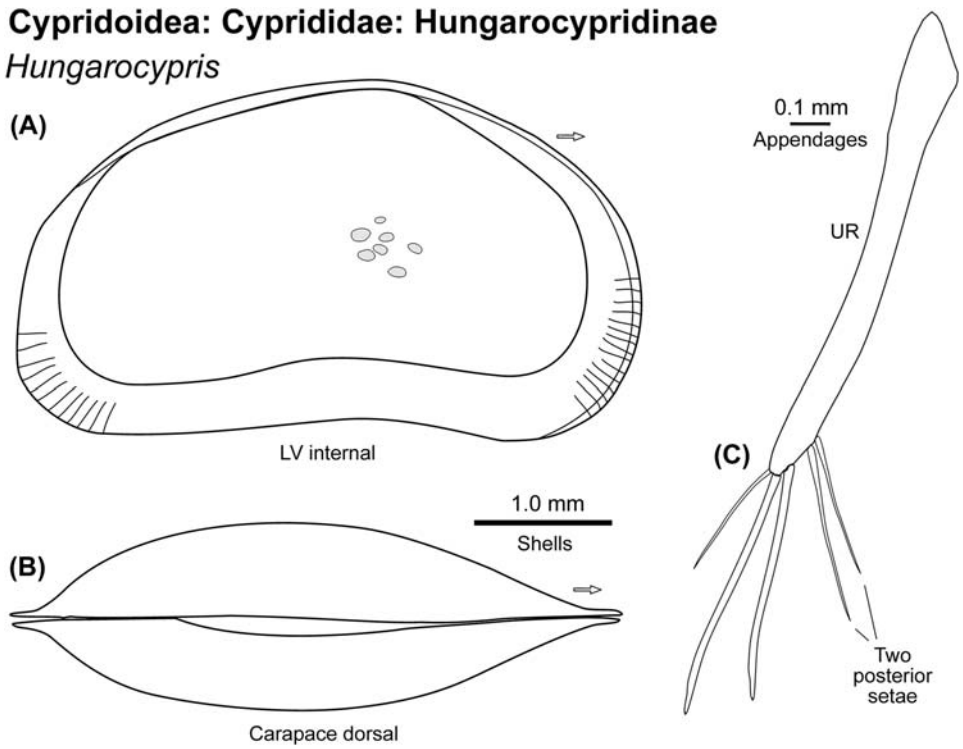


FIGURE 16.3.11 Key characteristics of the Cyprididae, subfamily Hungarocypridinae, genus *Hungarocypris*.

Ostracoda: Cypridoidea: Cyprididae: Cypricercinae: Genera

Savatenalinton & Martens (2009) described a new genus, *Bradleytriebella*, based on material from Thailand, which they distinguished from the closely related *Bradleystrandesia* by the absence of a d-seta on L5 (present in *Bradleystrandesia*), presence of a Wouters' Organ on A1 (absent in *Bradleystrandesia*) and a stouter, better-developed ventral branch on the UR attachment strut. However, Meisch (2000) showed the type-species of *Bradleystrandesia* as having the ventral branch well developed with a clavate distal end, while Savatenalinton & Martens (2009) showed it slender with a flattened, T-shaped distal end; in both cases the figured specimens were from Europe. In view of the difficulty in verifying the first two characters, both of which are very small when present, and uncertainty about (or variation in) the UR attachment strut, we have not included *Bradleytriebella* in the key.

1	Carapace ovoid in lateral view, inflated in dorsal/ventral view	2
1′	Carapace markedly elongate, laterally compressed (Figs. 16.3.18 A, B)	*Tanycypris*
2(1)	Carapace approximately symmetrical in anterior or posterior view	3
2′	Carapace markedly asymmetrical in anterior or posterior view, LV overhanging RV ventrally (Figs. 16.3.18 C–E)	*Bradleycypris*
3(2)	Triebel's Loop situated centrally in the proximal fork of the UR attachment strut (Figs. 16.3.18 F, G)	*Strandesia*
3′	Triebel's Loop situated on dorsal proximal branch of the UR attachment strut (Figs. 16.3.18 H–J)	*Bradleystrandesia*

Ostracoda: Cypridoidea: Cyprididae: Herpetocypridinae: Genera

1	Marginal zone without radial septa	2
1′	Marginal zone with conspicuous radial septa (Figs. 16.3.9 A–D)	*Stenocypris*
2(1)	Selvage peripheral/absent, inner list absent, in both valves	3
2′	Inwardly displaced selvage and/or inner list in at least one valve	6
3(2)	Posterior inner margin of CIL simply curved; UR posterior seta a short spine or inconspicuous seta or absent	4
3′	Posterior inner margin of CIL conspicuously sinuous; UR posterior seta long, conspicuous (Figs. 16.3.9 E, F)	*Stenocypria*
4(3)	UR weakly asymmetrical or symmetrical, posteriorly smooth or fringed with fine setules or spines	5
4′	UR conspicuously asymmetrical, posteriodistally fringed with prominent spines (Figs. 16.3.9 G–I)	*Chrissia*

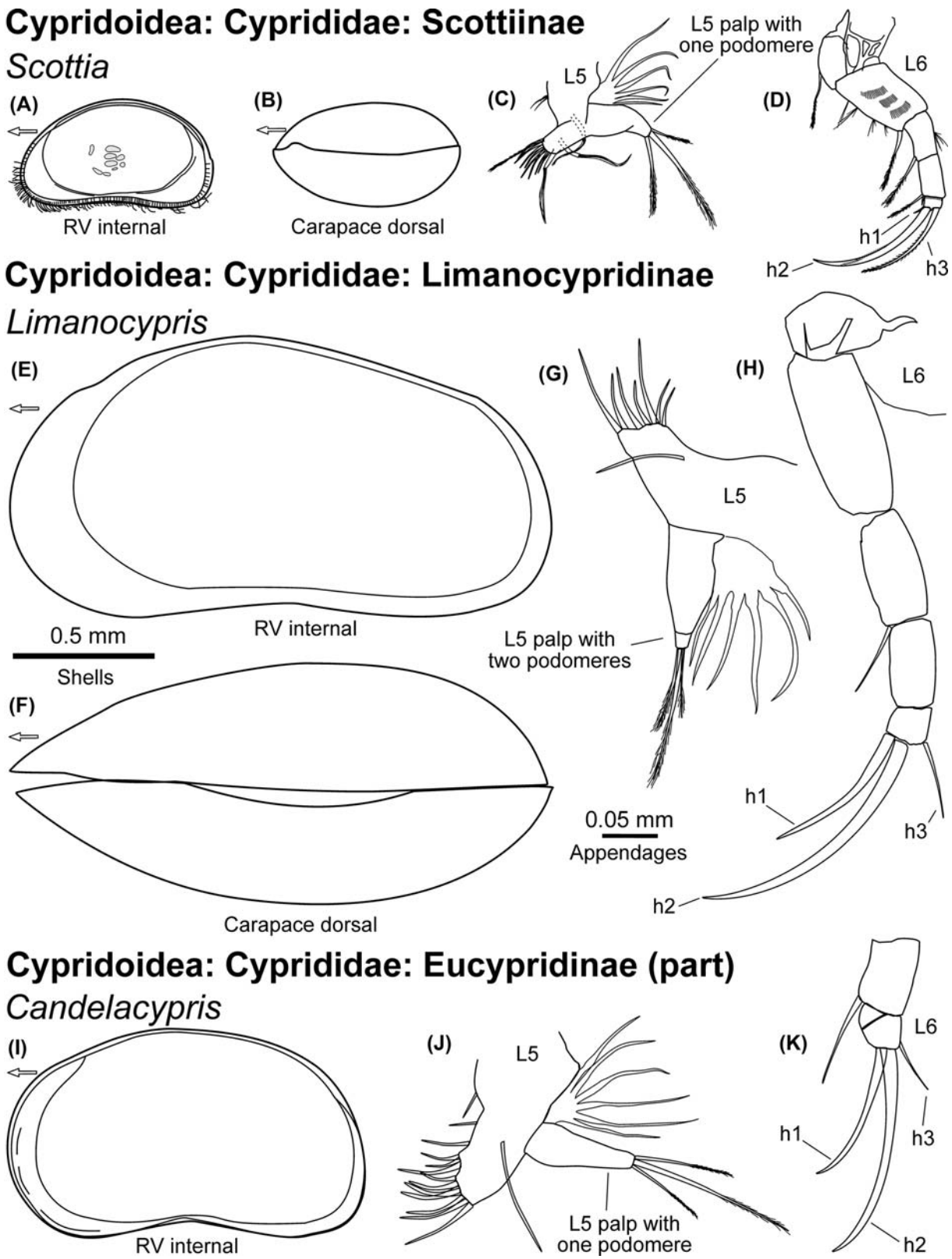


FIGURE 16.3.12 Key characteristics of genera of the Cyprididae, subfamilies Limanocypridinae, Scottiinae, and Eucypridinae (part).

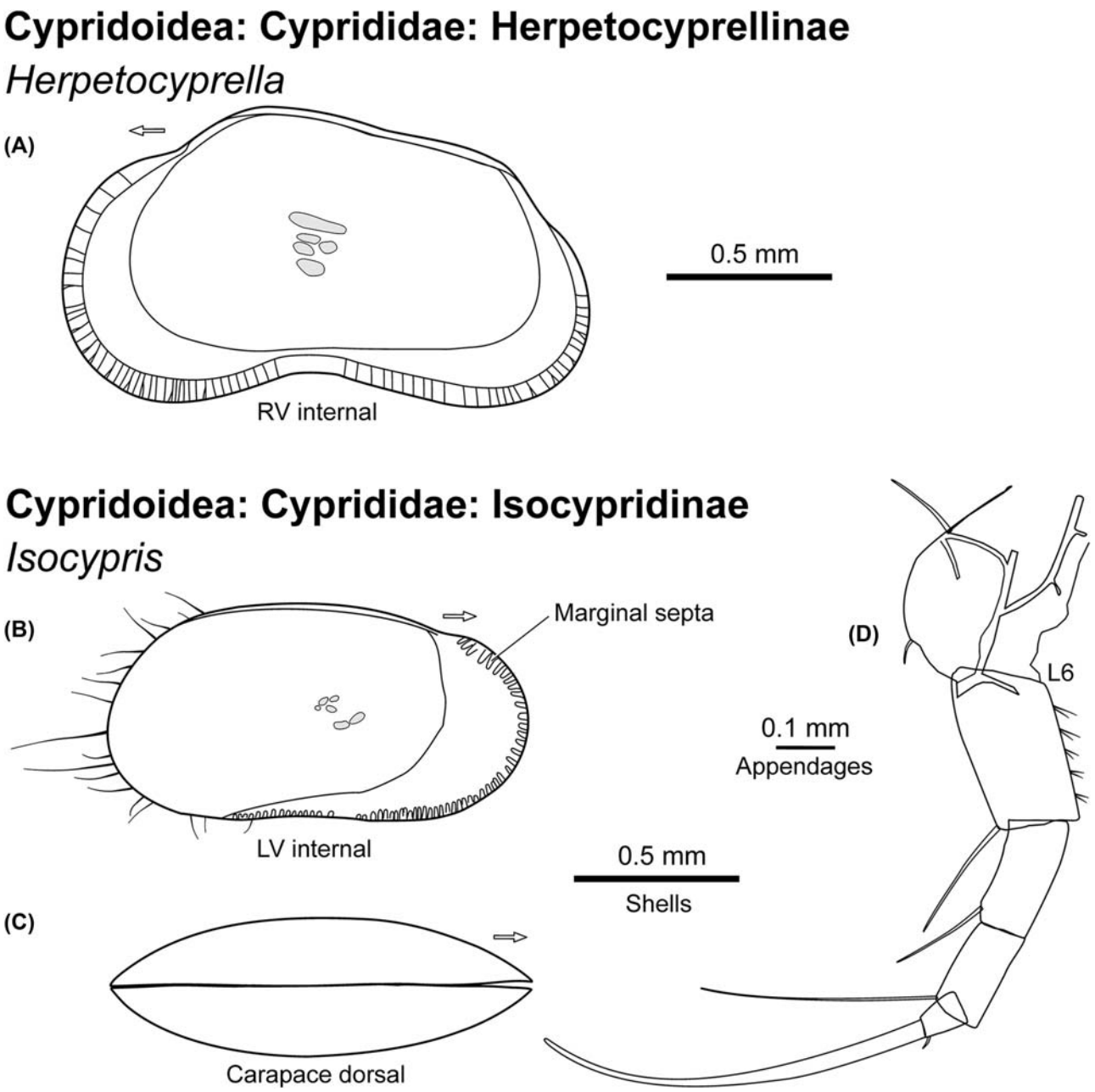


FIGURE 16.3.13 Key characteristics of genera of the Cyprididae, subfamilies Herpetocyprellinae and Isocypridinae.

5(4)	UR posterior seta absent (Fig. 16.3.9 J–L)	*Humphcypris*
5′	UR posterior seta small or transformed into a short spine (Figs. 16.3.9 M–O).	*Psychrodromus*
6(2)	Posterior selvage inwardly displaced in both valves or RV only	7
6′	Selvage inwardly displaced in LV, anteriorly and posteriorly; LV CIL with conspicuous inner list (Figs. 16.3.10 A–E)	*Herpetocypris*
7(6)	RV anterior selvage peripheral; LV anterior CIL with continuous inner list; L7 with one f-seta (Figs. 16.3.10 F–H)	*Ilyodromus*
7′	Anterior selvage inwardly displaced in RV only; LV anterior CIL with short inner list ventrally, truncated anteriorly; L7 with two f-setae (Figs. 16.3.10 I, J)	*Candonocypris*

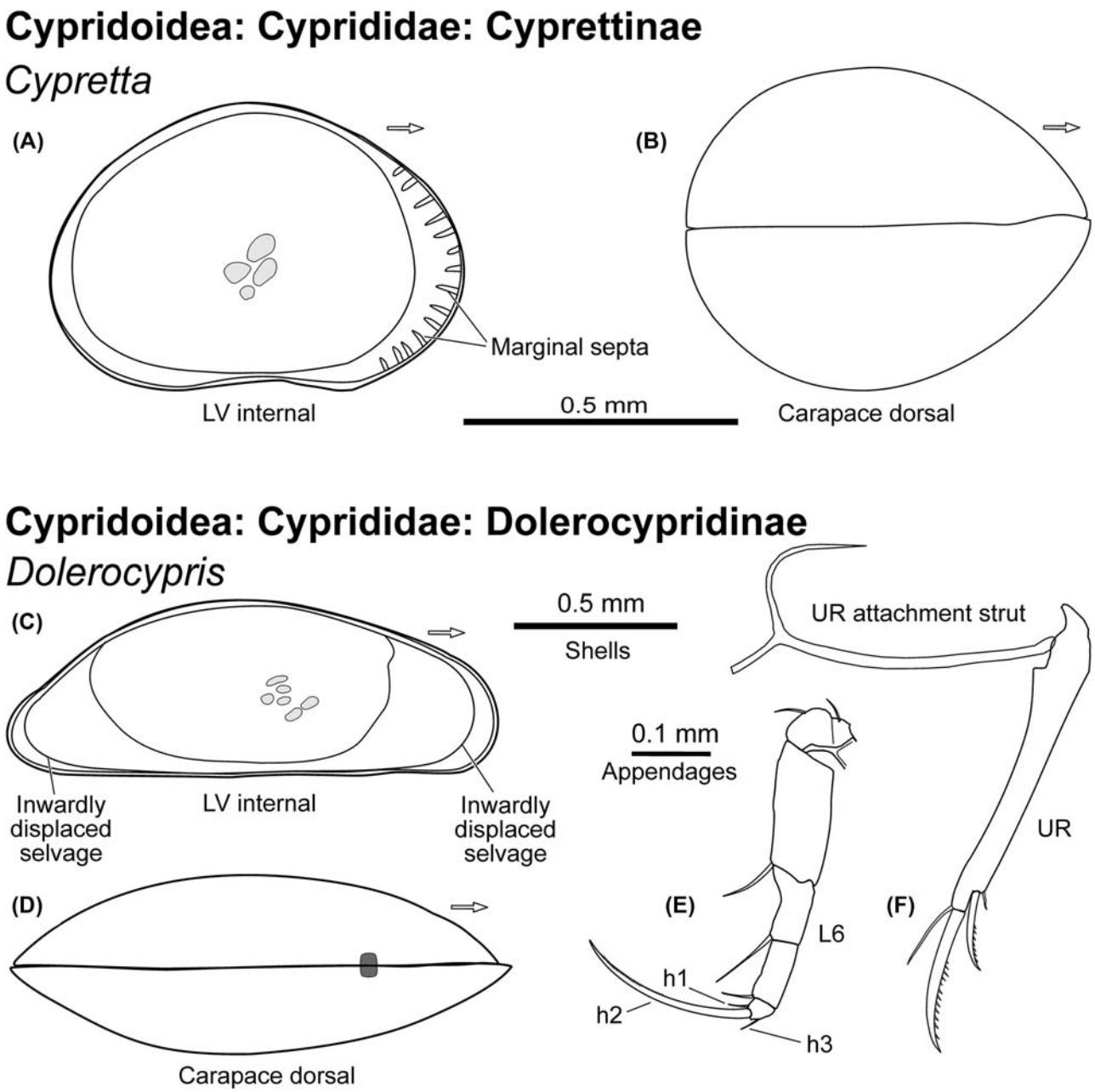


FIGURE 16.3.14 Key characteristics of genera of the Cyprididae, subfamilies Cyprettinae and Dolerocypridinae.

Ostracoda: Cypridoidea: Cyprididae: Cypridinae: Genera

1	L6 with five podomeres and two e-setae (Figs. 16.3.15 A, B)	*Chlamydotheca*
1′	L6 with four podomeres and one e-seta (Figs. 16.3.15 C, D)	*Cypris*

Ostracoda: Cypridoidea: Cyprididae: Cyprinotinae: Genera

1	RV with marginal blunt spines	2
1′	LV with marginal blunt spines (Fig. 16.3.16 A)	*Hemicypris*
2(1)	RV with a hump-like dorsal expansion (Fig. 16.3.16 B)	*Cyprinotus*
2′	RV without a hump-like dorsal expansion (although the LV may have one) (Fig. 16.3.16C)	*Heterocypris*

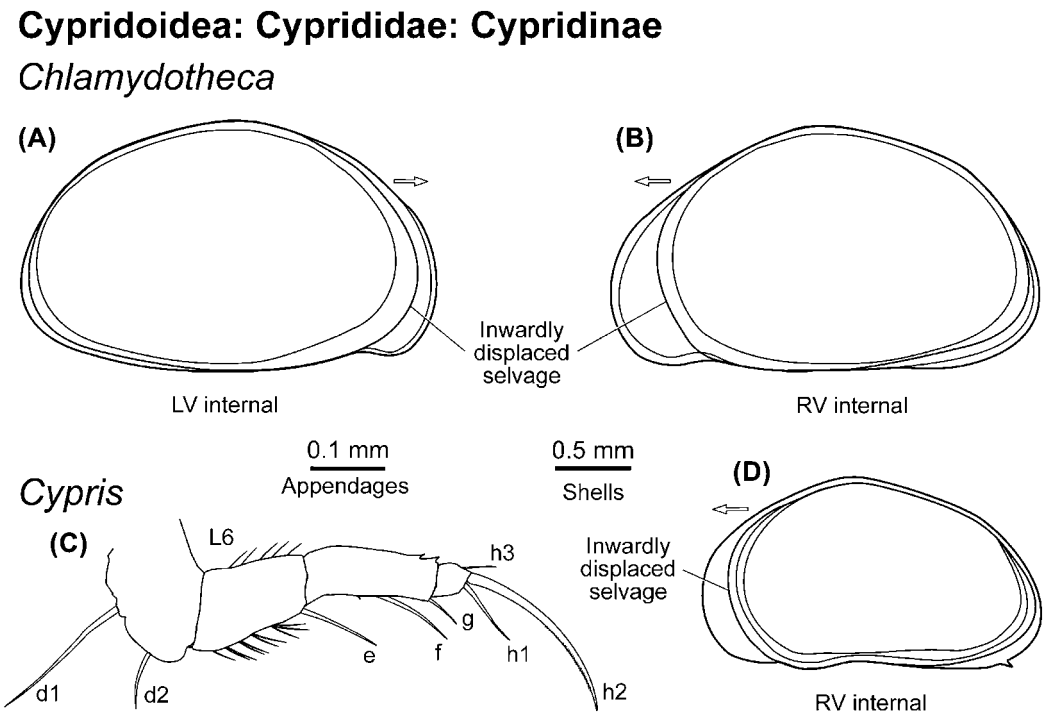


FIGURE 16.3.15 Key characteristics of genera of the Cyprididae, subfamily Cypridinae.

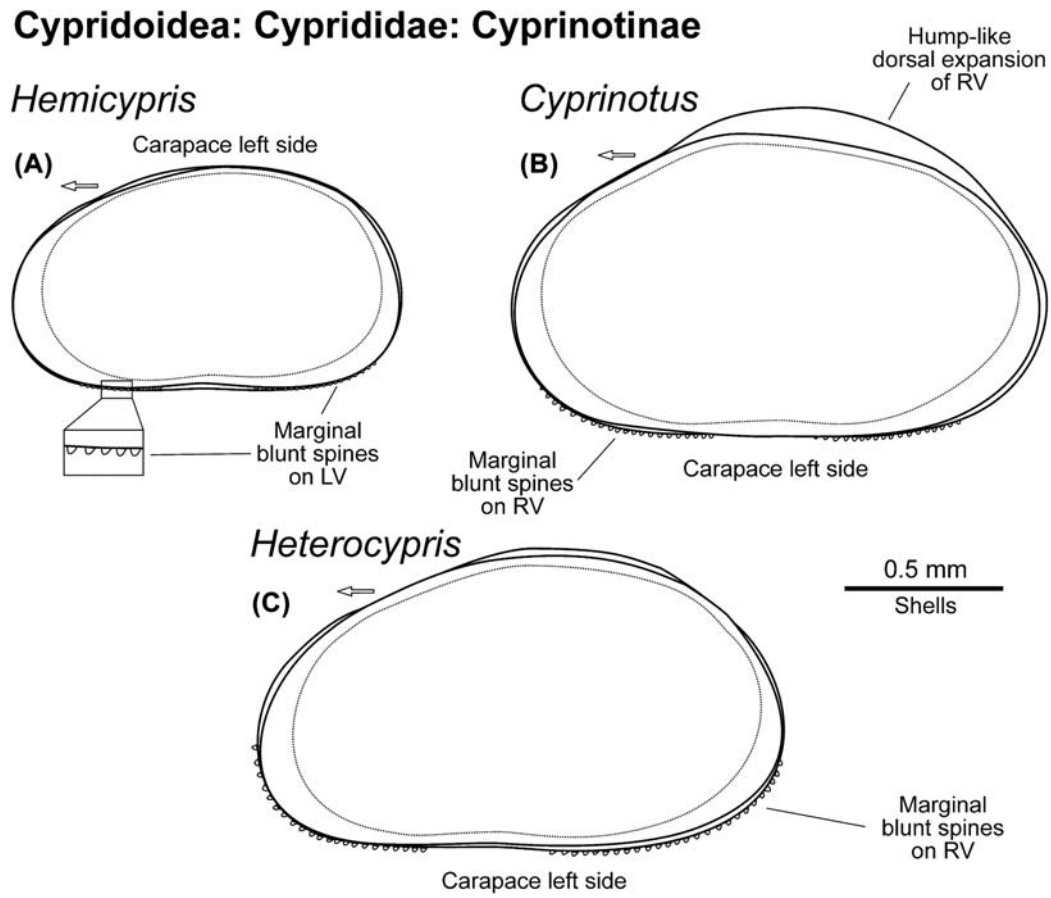


FIGURE 16.3.16 Key characteristics of genera of the Cyprididae, subfamily Cyprinotinae.

Ostracoda: Podocopida: Cypridoidea: Cyprididae: Eucypridinae: Genera

1	L6 with one terminal claw	2
1′	L6 with two terminal claws	*Candelacypris*
2(1)	LV CIL without an anteroventral internal tooth/peg; Mx1 outer endite with smooth or serrated bristles	3
2′	LV CIL with an anteroventral internal tooth/peg; Mx1 outer endite with serrated bristles (Figs. 16.3.17 A–C)	*Tonnacypris*
3(2)	Mx1 palp terminal podomere short or spatulate	4
3′	Mx1 palp terminal podomere elongate	6
4(3)	L6 with both d1-and d2-setae present	5
4′	L6 with only d1-seta present (Fig. 16.3.17 D)	*Amphicypris*
5(4)	RV anterior selvage inwardly displaced; LV selvage absent, CIL with prominent anterior inner list (Fig.16.3.17 E–F)	*Trajancypris*
5′	Selvage peripheral in both valves, CIL without inner lists (Fig. 16.3.17 G)	*Prionocypris*
6(3)	Selvage subperipheral, peripheral, or absent in both valves	7
6′	RV anterior selvage anteriorly inwardly displaced, LV selvage peripheral (Figs. 16.3.17 H, I)	*Koencypris*
7(6)	Anterior CIL with an inner list in the approximate middle, prominent in one or both valves	8
7′	Anterior CIL with an inner list, if present, not in the middle but distinctly closer to outer margin (Figs. 16.3.17 J, K)	*Eucypris*
8(7)	Mx1 outer endite with smooth bristles (Fig. 16.3.17 L)	*Eucyprinotus*
8′	Mx1 outer endite with serrated bristles (Figs. 16.3.17 M, N)	*Arctocypris*

Ostracoda: Cypridoidea: Candonidae: Subfamilies

Smith & Horne (2016) used the generic nomen *Candona sensu lato* because although other genera are widely employed (particularly *Fabaeformiscandona* and *Pseudocandona*), their diagnostic characters and the species that should be assigned to them are subjects of debate in the literature and it remains unclear where many species should be correctly assigned. For example, Karanovic (2012) regarded *Pseudocandona* as a subgenus of *Typhlocypris*, a point of view challenged by Namiotko et al. (2014), and placed in the genus *Eucandona* Daday, 1900 (not used herein) some of the species that were assigned by Meisch (2000) to *Fabaeformiscandona*. *Neglecandona* (not used herein) was introduced by Krstić (2006) to include a number of species extracted from *Candona s.l.* The key herein highlights *Candona s.l.* and then continues to key out *Candona sensu stricto* and other genera of the Candoninae, but it should be borne in mind that after couplet 6 the key is subject to unresolved taxonomic issues. The key does not include members of a candonine species flock endemic to Lake Baikal (Mazepova, 1990), many of which have externally ornamented shells, are currently assigned to the genera *Candona*, *Pseudocandona* and *Baicalocandona*, and are in need of revision.

1	Carapace short subovate in lateral view, with arched dorsal margin; length less than 1.5 times the height; A2 swimming setae present	**Cyclocypridinae**
1′	Carapace subtrapezoidal, subovate, or subreniform in lateral view, often elongate, dorsal margin arched or with a straight segment; length more than 1.5 times the height; A2 swimming setae absent	**Candoninae**

Ostracoda: Cypridoidea: Candonidae: Cyclocypridinae: Genera

1	Carapace compressed or weakly inflated in dorsal/ventral view; L7 penultimate podomere distal seta (g) short or absent	2
1′	Carapace strongly inflated (tumid) in dorsal/ventral view; L7 penultimate podomere distal seta (g) well developed (Figs. 16.3.19 A–D)	*Cyclocypris*
2(1)	RV with marginal pustules or denticles anteriorly and posteroventrally (Fig.16.3.19 E–G)	*Physocypria*
2′	Both valve margins smooth (Figs. 16.3.19 H–J)	*Cypria*

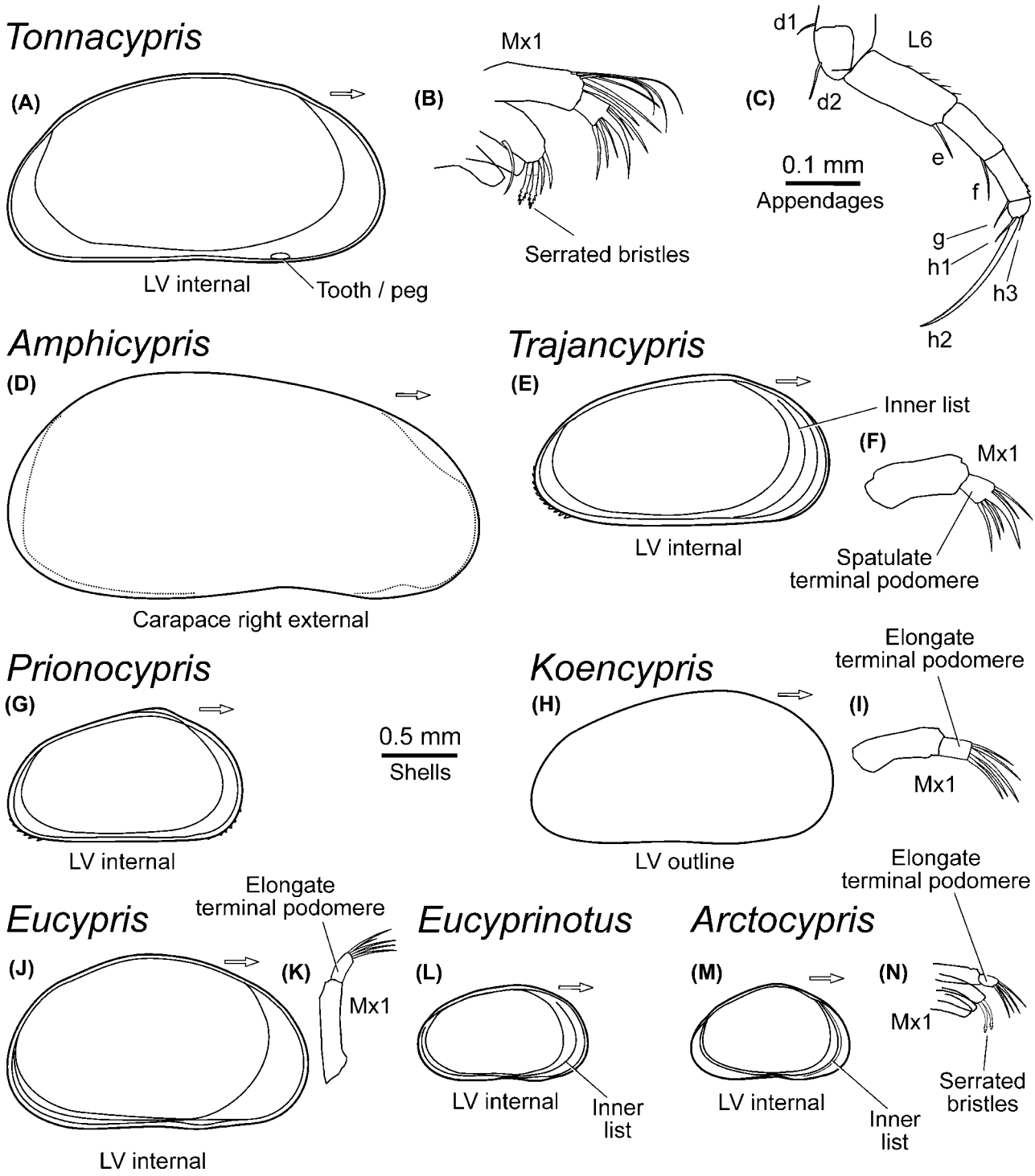


FIGURE 16.3.17 Key characteristics of genera of the Cypridae, subfamily Eucypridinae.

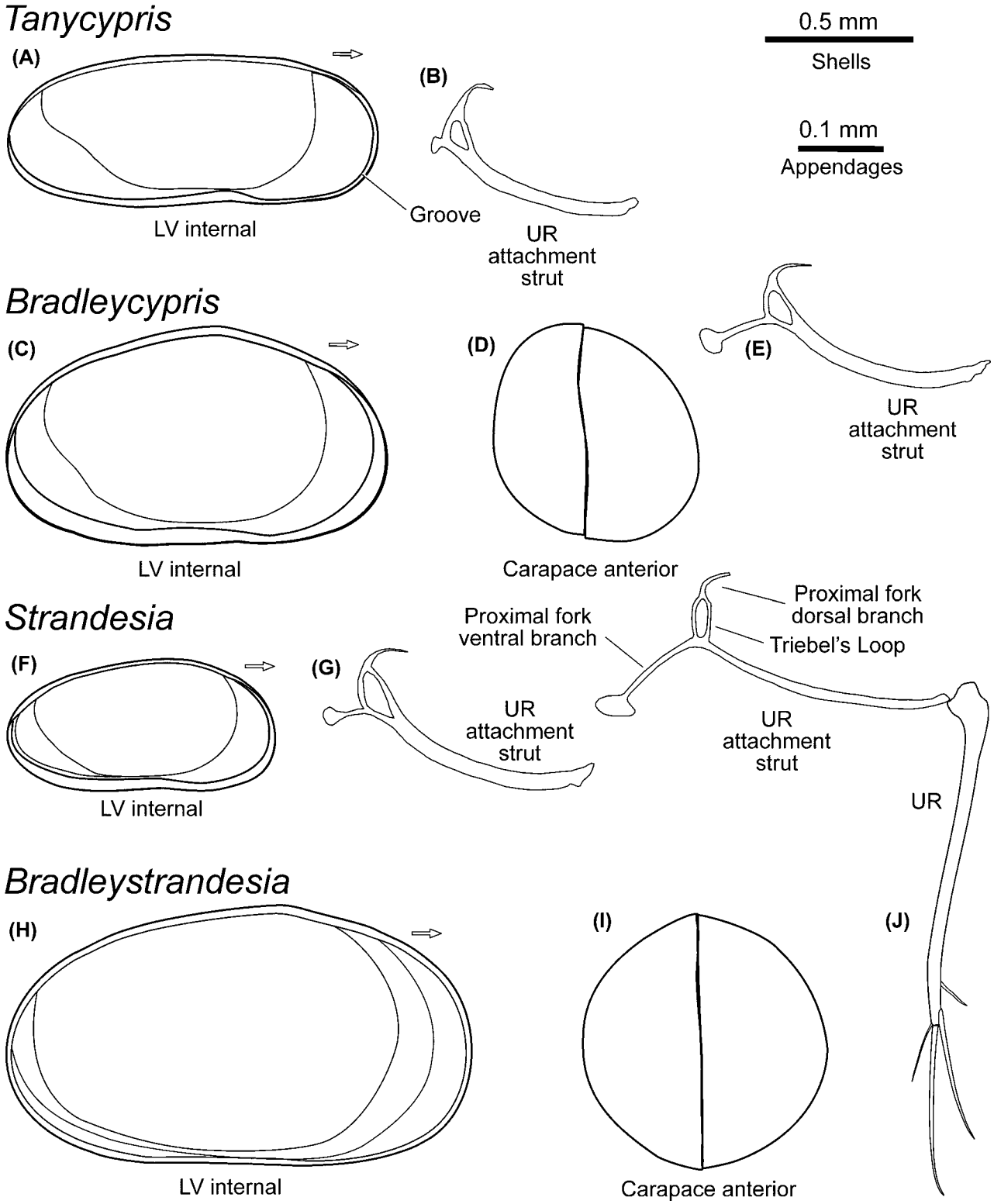


FIGURE 16.3.18 Key characteristics of genera of the Cyprididae, subfamily Cypricercinae.

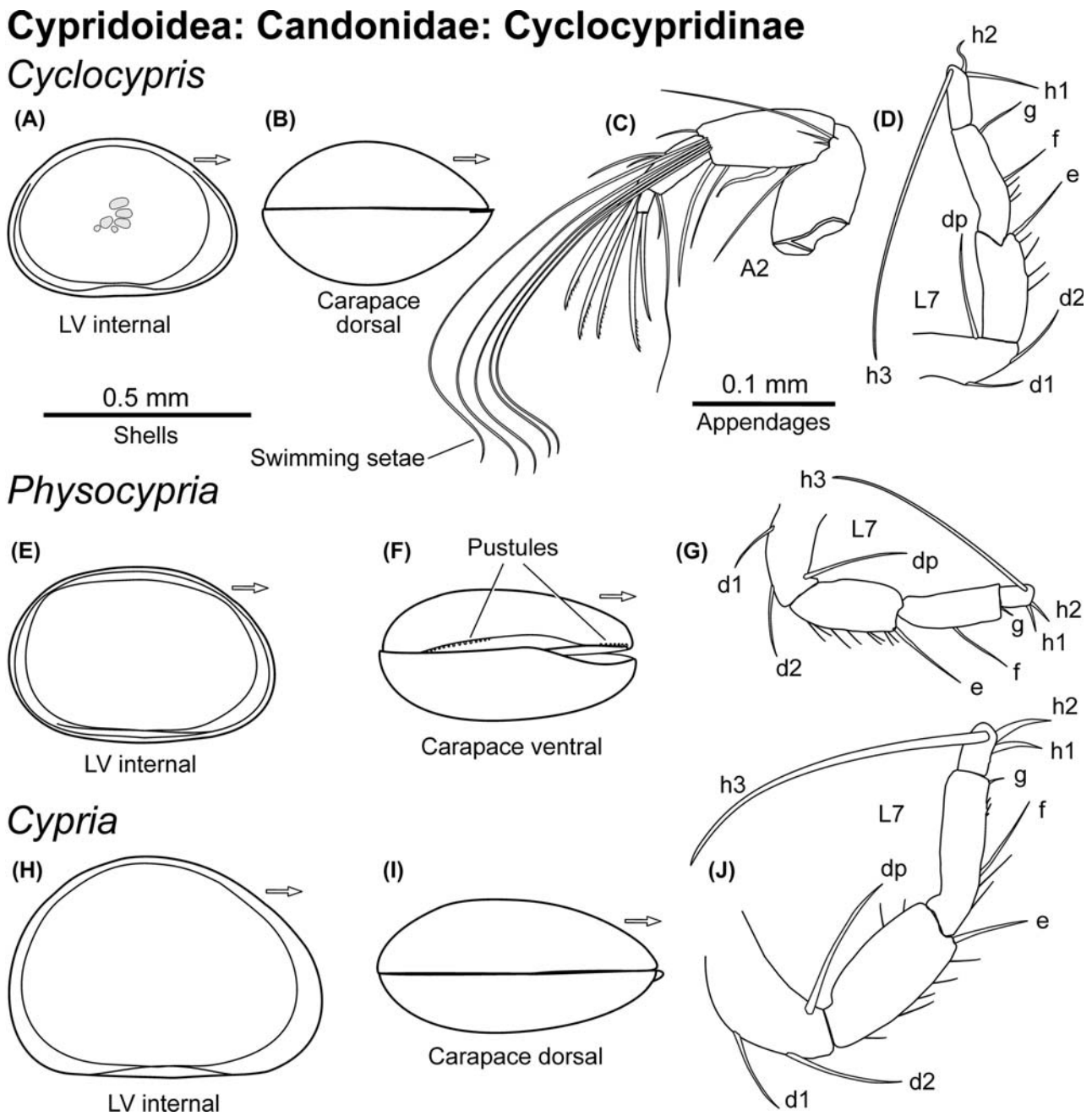


FIGURE 16.3.19 Key characteristics of genera of the Candonidae, subfamily Cyclocypridinae.

Ostracoda: Cypridoidea: Candonidae: Candoninae: Genera

At least one species of *Marococandona* has a reduced A1 with only five articulated podomeres and a reduced UR with only one terminal claw (Marmonier et al., 2005). These differences may merit the description of a new genus.

Earicandona and *Schellencandona* are very difficult to separate morphologically and differ mainly in adult size, with length of the former being >0.70 mm compared to <0.65mm for the latter. The example of the latter illustrated herein, has a shorter, more trapezoidal valve outline, but some species assigned to *Schellencandona* by Meisch (2000) have elongate valve outlines similar to those of species assigned to *Earicandona* by Karanovic (2013). If they were to be considered synonymous, the name *Schellencandona* would take priority.

1 Carapace external surface smooth or partially ornamented 2

1′ Carapace external surface entirely ornamented with fine net-like reticulation and pore conuli; moderately inflated with approximately parallel dorsal and ventral margins (Figs. 16.3.20 A, B) ..... *Paracandona*

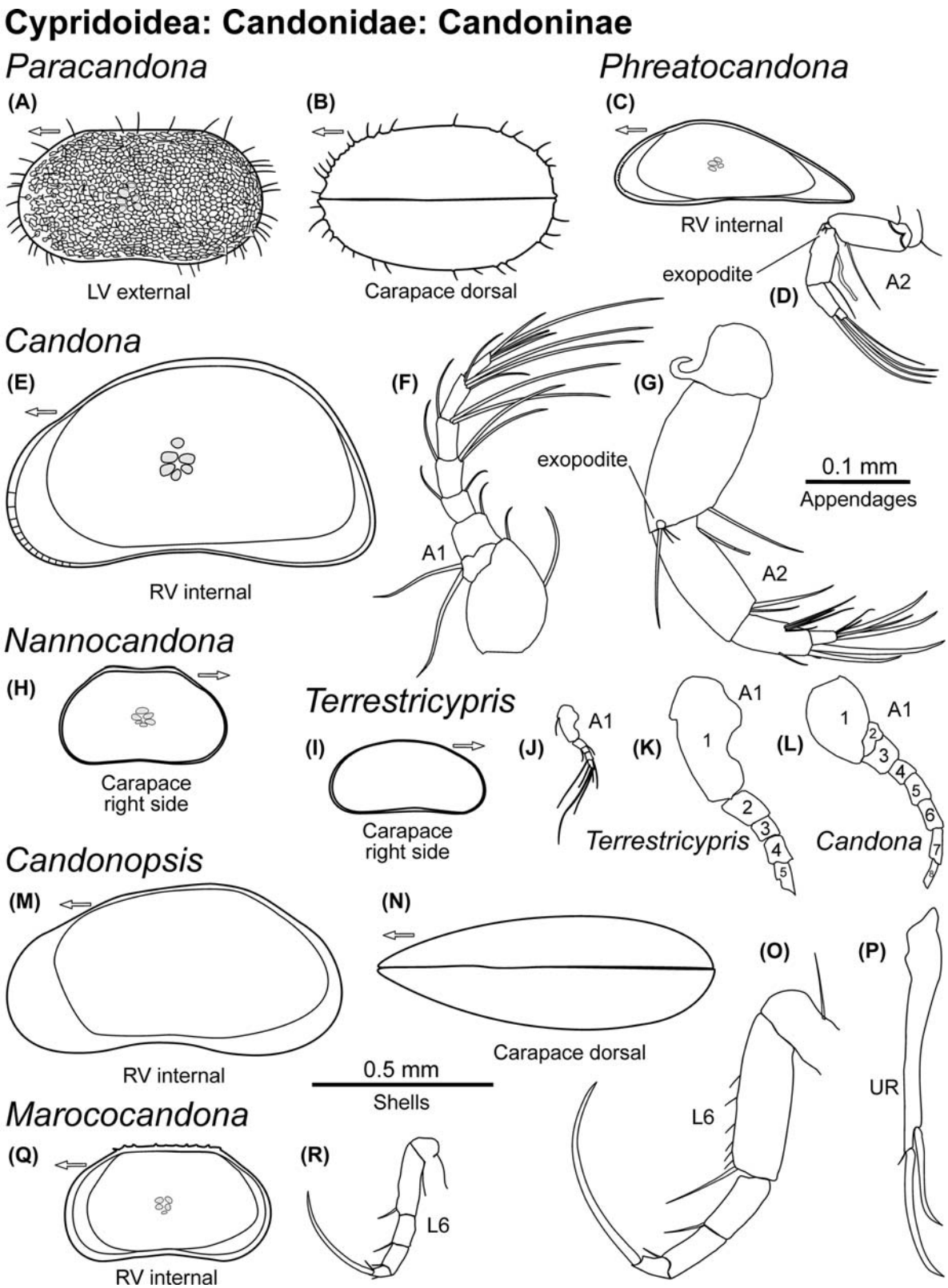


FIGURE 16.3.20 Key characteristics of genera of the Candonidae, subfamily Candoninae.

2(1)	A2 exopodite with one long and 1–2 very short setae; L6 penultimate podomere distal seta (g) shorter or no longer than the podomere 3
2′	A2 exopodite with three very short setae; L6 penultimate podomere distal seta (g) twice as long as the podomere (Figs. 16.3.20 C, D) ... *Phreatocandona*
3(2)	A1 with five articulated podomeres (Figs. 16.3.20 K) 4
3′	A1 with 7–8 articulated podomeres (Figs. 16.3.20 E–G, L) ..... *Candona sensu lato* 5
4(3)	Carapace subtrapezoidal in lateral view with a straight or weakly concave dorsal margin; Md palp second podomere with a group of three setae (Fig. 16.3.20 H). ..... *Nannocandona*
4′	Carapace subreniform in lateral view with a convex dorsal margin; Md palp second podomere with a group of four setae (Figs. 16.3.20 I, J) ..... *Terrestricypris*
5(3)	UR posterior seta absent 6
5′	UR posterior seta present 7
6(5)	Carapace subreniform in lateral view, L6 basal podomere with one seta (Figs. 16.3.20 M–P) ..... *Candonopsis*
6′	Carapace subrectangular in lateral view, L6 basal podomere without setae (Figs. 16.3.20 Q, R) ..... *Marococandona*
7(5)	L7 terminal podomere with two long and one short distal setae 8
7′	L7 terminal podomere with one long and two very short setae (Figs. 16.3.21 A, B) ..... *Mixtacandona*
8(7)	L7 penultimate podomere medial seta (f) absent 9
8′	L7 penultimate podomere medial seta (f) present (Figs. 16.3.21 C, D) ..... *Cryptocandona*
9(8)	L7 basal podomere with three setae..... 10
9′	L7 basal podomere with two setae 12
10(9)	Carapace subtriangular or subtrapezoidal in lateral view with maximum height close to mid-length 11
10′	Carapace subrectangular, subovate, or subreniform in lateral view, with maximum height well behind mid-length (Figs. 16.3.21 E, F) .. .. *Pseudocandona*
11(10)	Carapace subtriangular with an arched dorsal margin, conspicuously pitted in central dorsal area (Fig. 16.3.21 G) ..... *Typhlocypris*
11′	Carapace subtrapezoidal with arch of dorsal margin truncated forming a short straight or undulating section approximately parallel to the ventral margin (Figs. 16.3.21 H, I) ..... *Marmocandona*
12(9)	Md palp with smooth γ-seta 13
12′	Md palp with plumose γ-seta (Figs. 16.3.22 A, B) ..... *Candona sensu stricto*
13(12)	L6 basal podomere distal seta (d1) present 14
13′	L6 basal podomere distal seta absent (Figs. 16.3.22 C, D) ..... *Trajancandona*
14(13)	Posterodorsal margin of one or both valves with a lobate expansion or flap which overlaps the opposing valve margin when closed (Figs. 16.3.22 E–G) ..... *Fabaeformiscandona*
17′	Posterodorsal margins of valves simple, without lobate expansions (Figs. 16.3.22 H–J) ..... *Earicandona/Schellencandona*

Ostracoda: Cytheroidea: Families

The Cytheroidea is a diverse and predominantly marine group that also includes some nonmarine taxa. Only the Limnocytheridae and Kliellidae are exclusively nonmarine, but the Cytheridae, Cytherideidae, Leptocytheridae, Hemicytheridae, Loxoconchidae, and Xestoleberididae also have nonmarine representatives, occurring in fresh to hypersaline waters. In addition, the Entocytheridae (commensal on other crustaceans) are mainly nonmarine but include some marine/brackish taxa. Cytheroideans are benthonic nonswimming ostracods that crawl, climb, or burrow (epifaunal, infaunal, interstitial, or commensal).

While couplet 3 is effective for freshwater members of the families, most of the very diverse marine/brackish water members of the Hemicytheridae and Leptocytheridae would key out incorrectly here; for example the leptocytherid genus *Leptocythere* has branching marginal pore canals in bunches and the hemicytherid genus *Hemicythere* has simple ones, but neither occurs in fresh water.

The carapace is smooth or ornamented, sometimes strongly, with the dorsal margin often bearing a robust and complex hinge structure that is rarely adont. Carapace size and shape variable, with strong sexual dimorphism in some genera. Calcified inner lamella usually well developed. The basic AMS pattern is four or five scars in a vertical row. Lateral ocelli of median eye often with corresponding eyespots or eye tubercles developed in the valves. Normal pores are both simple and sieve-type (the latter present in most but not all families). A1 with five to seven articulated podomeres. A2 endopodite with three to four articulated podomeres; the exopodite is a jointed or unjointed spinneret seta connected to a gland at the base of the limb and is sometimes sexually dimorphic. Md palp is a small branchial plate with up to seven rays. Mx1 branchial plate has up to four reflexed, forward-pointing rays. L5, L6, and L7 are walking legs similar in structure and direction, each with three endopodite podomeres and a terminal claw (which is fused with the "missing" fourth podomere); these limbs are sometimes sexually dimorphic. The L5 branchial plate has up to four rays in some genera but typically reduced to one or two setae and sometimes absent. UR is reduced or absent. Male copulatory appendages have an incorporated sperm pump (no Zenker's organ). Females of a few families or subfamilies have an expanded posterior brood chamber, but most do not.

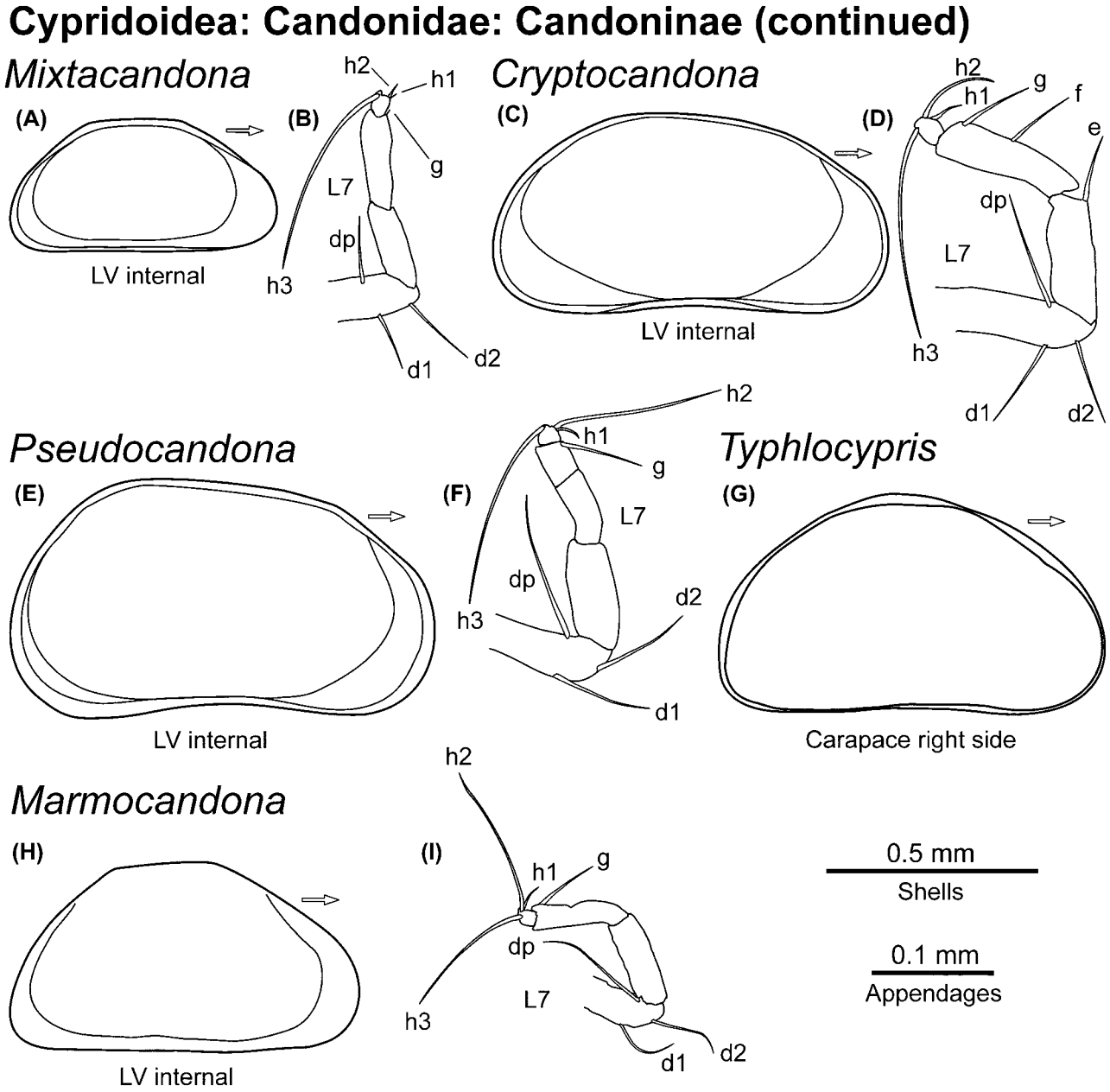


FIGURE 16.3.21 Key characteristics of genera of the Candonidae, subfamily Candoninae (continued).

1	Carapace well or weakly calcified, externally smooth or ornamented; L5, L6, and L7 with long terminal claws (distinctly longer than terminal podomere)	2
1′	Carapace weakly calcified, sometimes flattened anteroventrally, unornamented; L5, L6, and L7 with short, hooked terminal claws (no longer than terminal podomere) bearing short spines; commensal or ectoparasitic on larger crustaceans	**Entocytheridae**
2(1)	Carapace external surface smooth or ornamented, Xestoleberis-spot absent	3
2′	Carapace external surface smooth, Xestoleberis-spot present (Fig. 16.3.23 E)	Xestoleberididae, one genus: *Xestoleberis*
3(2)	Anterior marginal pore canals mostly simple (a few may be bifurcated) or not discernable	4
3′	Anterior marginal pore canals conspicuously arranged in brush-like bunches (Fig. 16.3.23 F)	Hemicytheridae, one genus: *Tyrrhenocythere*

Cypridoidea: Candonidae: Candoninae (continued)

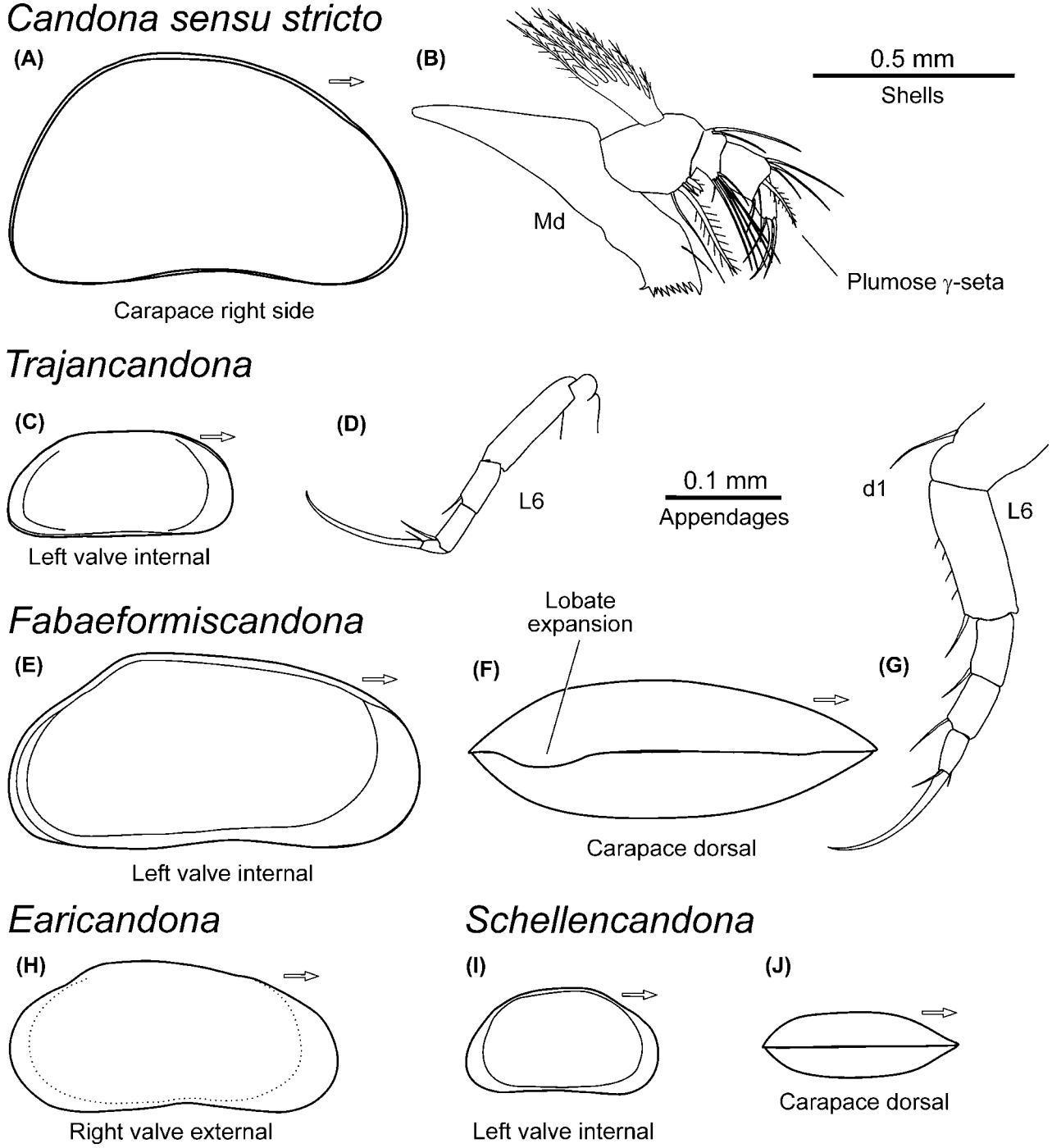


FIGURE 16.3.22 Key characteristics of genera of the Candonidae, subfamily Candoninae (continued).

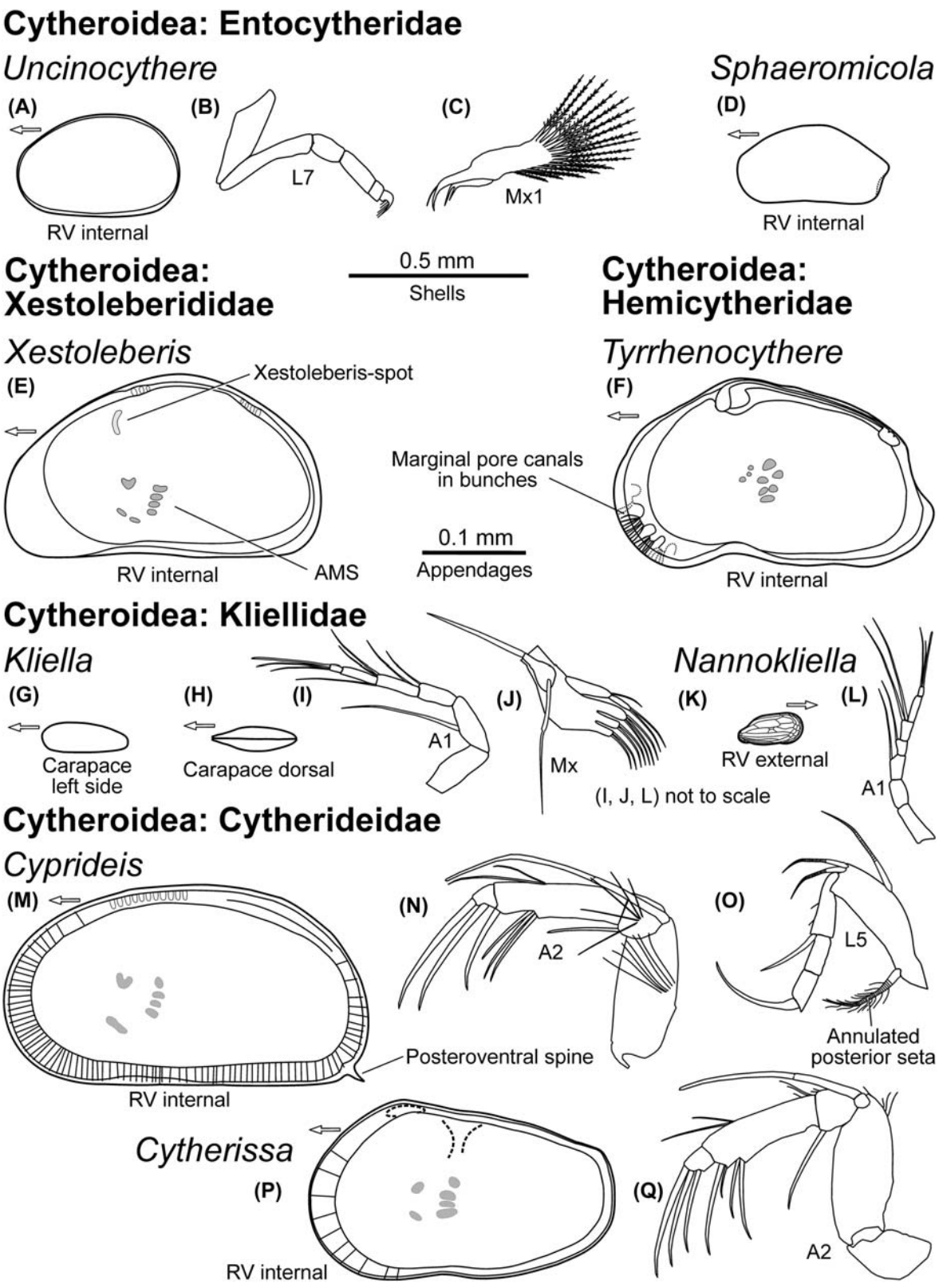


FIGURE 16.3.23 Key characteristics of genera of Cytheroidea.

4(3)	Mx1 branchial plate with >10 rays	5
4′	Mx1 branchial plate with only 1−2 rays	**Kliellidae**
5(4)	L5 and L6 basal podomere posterior setae (exopodites) slender or reduced, not annulated	6
5′	L5 and L6 basal podomere posterior setae (exopodites) stout, conspicuously annulated	**Cytherideidae**
6(5)	A2 with two terminal claws	7
6’	A2 with one to three terminal claws	**Limnocytheridae**
7(6)	Hinge gongylodont (RV posterior tooth bilobate) or henodont (RV posterior tooth simple)	**Loxoconchidae**
7′	Hinge entomodont (RV posterior tooth with five cusps increasing in size toward posterior) (Fig. 16.3.26 I)	Leptocytheridae, one genus: *Amnicythere*

Ostracoda: Cytheroidea: Entocytheridae: Genera

1	Mx1 with a branchial plate (Figs. 16.3.23 A−C)	Entocytherinae, one genus: *Uncinocythere*
1′	Mx1 without a branchial plate (Fig. 16.3.23 D)	Sphaeromicolinae, one genus: *Sphaeromicola*

Cytheroidea: Kliellidae: Genera

1	Carapace smooth, A1 with six articulated podomeres (Figs. 16.3.23 G−J)	*Kliella*
1′	Carapace ornamented, A1 with seven articulated podomeres (Figs. 16.3.23 K, L)	*Nannokliella*

Ostracoda: Cytheroidea: Cytherideidae: Genera

The genus *Cytherissa* has one Holarctic species and c. 60 Palaearctic species endemic to Lake Baikal.

1	RV with a small posteroventral spine; A2 with two terminal claws (Figs. 16.3 23 M−O)	*Cyprideis*
1′	RV without a posteroventral spine; A2 with three terminal claws (Figs. 16.3.3 and 16.3.23 P−Q)	*Cytherissa*

Ostracoda: Cytheroidea: Limnocytheridae: Subfamilies

1	Female carapace without a posterior brood chamber	**Limnocytherinae**
1′	Female carapace swollen posteriorly to form a brood chamber for eggs and juveniles	**Timiriaseviinae**

Ostracoda: Cytheroidea: Limnocytheridae: Limnocytherinae: Genera

Several genera (listed in Table 16.3.1) have been separated from *Limnocythere* by various authors, in some cases as subgenera that have later been elevated to full generic status by others. In cases where these taxa are distinguished only by adult male characteristics, we have been unable to devise a useful key based on adult female characters. For example, the subgenus *Limnocythere* (*Limnocytherina*) Negadaev-Nikonov, 1967, elevated to generic level by some authors (e.g., Martens, 1996; Meisch, 2000), is mainly distinguished from *Limnocythere* (*Limnocythere*) Brady, 1868 by structural features of the male copulatory appendages; consequently recognizing it can be difficult (and impossible in extinct fossil species for which appendages are unknown). Delorme (1971) used both subgenera for North American limnocytherid species, but did not explain the criteria used to separate them and subsequently (Delorme, 2001; Smith & Delorme, 2010) used only the genus *Limnocythere*. Similarly, *Potamocythere* Schornikov, 1986 and *Limnocythere* (*Galo-limnocythere*) Schornikov, 1986 (the latter elevated to generic rank by Martens, 1996) are only separable from *Limnocythere* by details of male appendage morphology. For the purposes of the key, we use *Limnocythere s.l.* to accommodate these taxa.

Leucocythere Kaufmann, 1892 and *Athalocythere* Schornikov, 1986 can be separated from *Limnocythere* by details of the hinge structure, but may only be distinguished from each other by details of male appendage morphology, so we have accommodated them both in *Leucocythere s.l.*

1	All marginal pore canals short and simple	2
1′	Marginal pore canals long, some bifurcated (Fig. 16.3.24 F, G)	*Paralimnocythere*
2(1)	RV hinge with anterior and posterior teeth well developed; LV hinge with a smooth median bar (Fig. 16.3.24 A−E)	*Limnocythere sensu lato*
2′	RV hinge with a trilobate posterior tooth, anterior tooth weakly developed; LV hinge with a crenulate median bar (Fig. 16.3.24 H−J)	*Leucocythere sensu lato*

TABLE 16.3.1 Taxonomic Checklist of Palaearctic Free-living and Commensal Freshwater Ostracod Genera

Class Ostracoda Latreille, 1806 (=Ostrachoda Latreille, 1802)
Subclass Podocopa Sars, 1866
Order Podocopida Sars, 1866
Suborder Cypridocopina Jones, 1901
Superfamily Cypridoidea Baird, 1845
Family Cyprididae Baird, 1845
Subfamily Cyprettinae Hartmann, 1963
Genus *Cypretta* Vávra, 1895
Subfamily Cypricercinae McKenzie, 1971
Genus *Bradleycypris* McKenzie, 1982
Genus *Bradleystrandesia* Broodbakker, 1983
Genus *Bradleytriebella* Savatenalinton & Martens, 2009
Genus *Strandesia* Vávra, 1895
Genus *Tanycypris* Triebel, 1959
Subfamily Cypridinae Baird, 1845
Genus *Chlamydotheca* Saussure, 1858
Syn.: *Pachycypris* Claus, 1892
Genus *Cypris* O. F. Müller, 1776
Subfamily Cypridopsinae Kaufmann, 1900
Genus *Cavernocypris* Hartmann, 1964
Genus *Cypridopsis* Brady, 1867
Genus *Plesiocypridopsis* Rome, 1965
Genus *Potamocypris* Brady, 1870
Genus *Pseudocypridopsis* Karanovic, 1999
Genus *Sarscypridopsis* McKenzie, 1977
Subfamily Cyprinotinae Bronstein, 1947
Genus *Cyprinotus* Brady, 1886
Genus *Hemicypris* Sars, 1903
Genus *Heterocypris* Claus, 1892
Subfamily Dolerocypridinae Triebel, 1961
Genus *Dolerocypris* Kaufmann, 1900
Subfamily Eucypridinae Bronstein, 1947
Genus *Amphicypris* Sars, 1901
Genus *Arctocypris* Petkovski, Scharf & Keyser, 2016
Genus *Candelacypris* Baltanás, 2001
Genus *Eucyprinotus* Sywula, 1972
Genus *Eucypris* Vávra, 1891
?Syn.: *Candocyprinotus* Delorme, 1970

TABLE 16.3.1 Taxonomic Checklist of Palaearctic Free-living and Commensal Freshwater Ostracod Genera—cont'd

Genus *Koencypris* Meisch, 2000
Genus *Prionocypris* Brady & Norman, 1896
Genus *Tonnacypris* Diebel & Pietrzeniuk, 1975
Genus *Trajancypris* Martens, 1989
Subfamily Herpetocyprellinae Bronstein, 1947
Genus *Herpetocyprella* Daday, 1909
Subfamily Herpetocypridinae Kaufmann, 1900
Syn.: Stenocypridinae Ferguson, 1964
Tribe Herpetocypridini Kaufmann, 1900
Genus *Candonocypris* Sars, 1894
Genus *Herpetocypris* Brady & Norman, 1889
Syn.: *Erpetocypris* Brady & Norman, 1889
Syn.: *Siphlocandona* Brady, 1910
Genus *Ilyodromus* Sars, 1894
Tribe Psychrodromini Martens, 2001
Genus *Humphcypris* Martens, 1997
Genus *Psychrodromus* Danielopol & McKenzie, 1977
Tribe Stenocypridini Ferguson, 1964
Genus *Chrissia* Hartmann, 1957
Syn.: *Gesa* Hartmann, 1957
Syn.: *Parastenocypris* Hartmann, 1964
Genus *Stenocypria* G. W. Müller, 1901
Genus *Stenocypris* Sars, 1889
Subfamily Hungarocypridinae Bronstein, 1947
Genus *Hungarocypris* Vávra, 1906
Subfamily Isocypridinae Rome, 1965
Genus *Isocypris* G.W. Müller, 1908
Subfamily Scottiinae Bronstein, 1947
Genus *Scottia* Brady & Norman, 1889
Subfamily Limanocypridinae Hartmann & Puri, 1974
Genus *Limanocypris* Schornikov, 1961
Family Candonidae Kaufmann, 1900
Subfamily Candoninae Kaufmann, 1900
Tribe Candonini Kaufmann, 1900
Genus *Baicalocandona* Mazepova, 1976
Genus *Candona* Baird, 1845
Genus *Cryptocandona* Kaufmann, 1900
Genus *Earicandona* Karanovic, 2013

(*Continued*)

TABLE 16.3.1 Taxonomic Checklist of Palaearctic Free-living and Commensal Freshwater Ostracod Genera—cont'd

- Genus *Fabaeformiscandona* Krstić, 1972
- Genus *Marmocandona* Danielopol, Namiotko, & Meisch, 2012
- Genus *Mixtacandona* Klie, 1938
- Syn.: *Trapezicandona* Schornikov, 1969
- Genus *Nannocandona* Ekman, 1914
- Genus *Paracandona* Hartwig, 1899
- Genus *Phreatocandona* Danielopol, 1973
- Genus *Pseudocandona* Kaufmann, 1900
- Genus *Schellencandona* Meisch, 1996
- Genus *Trajancandona* Karanovic, 1999

Tribe Candonopsini Karanovic, 2004

- Genus *Candonopsis* Vávra, 1891

Tribe Terrestricypridini Schornikov, 1980

- Genus *Terrestricypris* Schornikov, 1980

Subfamily Cyclocypridinae Kaufmann, 1900

- Genus *Cyclocypris* Brady & Norman, 1889
- Genus *Cypria* Zenker, 1854
- Syn.: *Bentocypria* Kovalenko, 1987
- Genus *Physocypria* Vávra, 1897

Family Ilyocyprididae Kaufmann, 1900

Subfamily Ilyocypridinae Kaufmann, 1900

- Genus *Ilyocypris* Brady & Norman, 1889

Family Notodromadidae Kaufmann, 1900

Subfamily Cyproidinae Hartmann, 1963

- Genus *Cyprois* Zenker, 1854

Subfamily Notodromadinae Kaufmann, 1900

- Genus *Notodromas* Lilljeborg, 1853

Suborder Darwinulocopina Sohn, 1988

Superfamily Darwinuloidea Brady & Norman, 1889

Family Darwinulidae Brady & Norman, 1889

- Genus *Darwinula* Brady & Robertson, 1885
- Genus *Microdarwinula* Danielopol, 1969
- Genus *Penthesilenula* Rossetti & Martens, 1998
- Genus *Vestalenula* Rossetti & Martens, 1998

Suborder Cytherocopina Gründel, 1967

Superfamily Cytheroidea Baird, 1850

Family Cytherideidae Sars, 1925

Subfamily Cytherideinae Sars, 1925

Tribe Cytherideini Kollmann, 1960

TABLE 16.3.1 Taxonomic Checklist of Palaearctic Free-living and Commensal Freshwater Ostracod Genera—cont'd

- Genus *Cyprideis* Jones, 1857
- Genus *Cytherissa* Sars, 1925

Family Entocytheridae Hoff, 1942

Subfamily Entocytherinae Hoff, 1942

- Genus *Uncinocythere* Hart, 1962

Subfamily Sphaeromicolinae Hart, 1962

- Genus *Sphaeromicola* Paris, 1916

Family Hemicytheridae Puri, 1953

Subfamily Hemicytherinae Puri, 1953

- Genus *Tyrrhenocythere* Ruggieri, 1955

Family Kliellidae Schäfer, 1945

- Genus *Kliella* Schäfer, 1945
- Genus *Nannokliella* Schäfer, 1945

Family Leptocytheridae Hanai, 1957

Subfamily Leptocytherinae Hanai, 1957

- Genus *Amnicythere* Devoto, 1975

Family Limnocytheridae Sars, 1928

Subfamily Limnocytherinae Sars, 1928

Tribe Leucocytherini Danielopol & Martens, 1989

- Genus *Athalocythere* Schornikov, 1986
- Genus *Leucocythere* Kaufmann, 1892

Tribe Limnocytherini Sars, 1928

- Genus *Galolimnocythere* Schornikov, 1973
- Genus *Limnocythere* Brady, 1867
- Genus *Limnocytherina* Negadaev-Nikonov, 1967
- Genus *Paralimnocythere* Carbonnel, 1965
- Genus *Potamocythere* Schornikov, 1986

Subfamily Timiriaseviinae Mandelstam, 1960

- Syn.: Metacypridinae Danielopol, 1960
- Genus *Dolekiella* Gidó, Artheau, Colin, Danielopol & Marmonier, 2007
- Genus *Frambocythere* Colin, 1981
- Genus *Kovalevskiella* Klein, 1963
- Genus *Metacypris* Brady & Robertson, 1870

Family Loxoconchidae Sars, 1925

- Genus *Cytheromorpha* Hirschmann, 1909
- Genus *Loxoconcha* Sars, 1866
- Genus *Pseudolimnocythere* Klie, 1938

Family Xestoleberididae Sars, 1928

- Genus *Xestoleberis* Sars, 1866

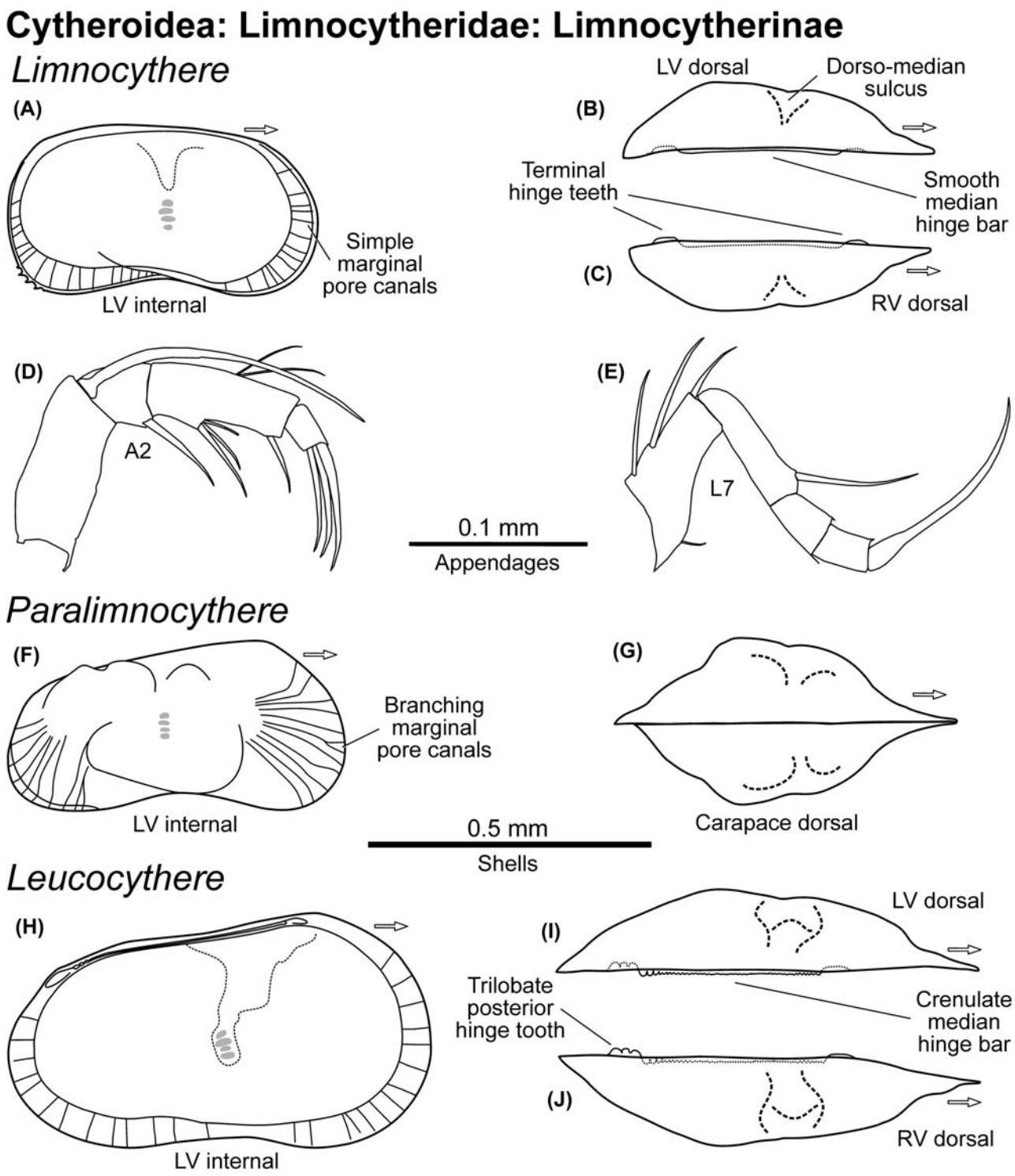


FIGURE 16.3.24 Key characteristics of genera of the Limnocytheridae, subfamily Limnocytherinae.

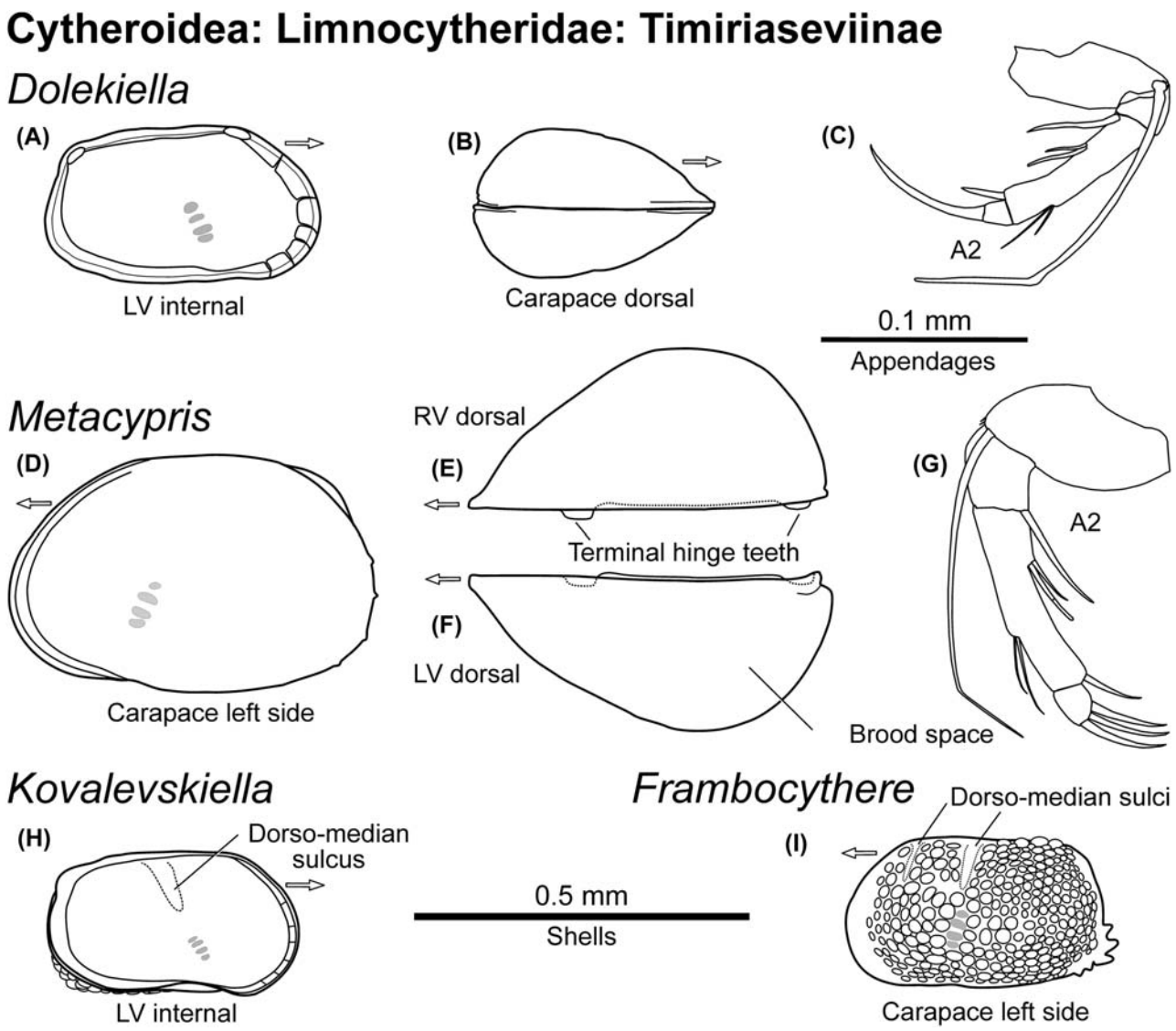


FIGURE 16.3.25 Key characteristics of genera of the Limnocytheridae, subfamily Timiriaseviinae.

Cytheroidea: Limnocytheridae: Timiriaseviinae: Genera

The interstitial genera *Kovalvskiella* and *Frambocythere* are closely related and are separable only by the number of dorsomedian sulci, the anterior of which (in *Frambocythere*) may be weakly developed and difficult to observe (Smith et al. 2012).

1	A2 with three terminal claws	2
1′	A2 with one terminal claw (Figs. 16.3.25 A–C)	*Dolekiella*
2(1)	Hinge inverse lophodont (LV with terminal teeth), carapace external surface ornamented with small closely spaced pustules and with 1–2 dorsomedian sulci in each valve	3
2′	Hinge lophodont (RV with terminal teeth), carapace external surface smooth or finely pitted and without dorsomedian sulci (Figs. 16.3.25 D–G)	*Metacypris*
3(2)	Each valve with one dorsomedian sulcus (Fig. 16.3.25 H)	*Kovalevskiella*
3′	Each valve with two dorsomedian sulci (Fig. 16.3.25 I)	*Frambocythere*

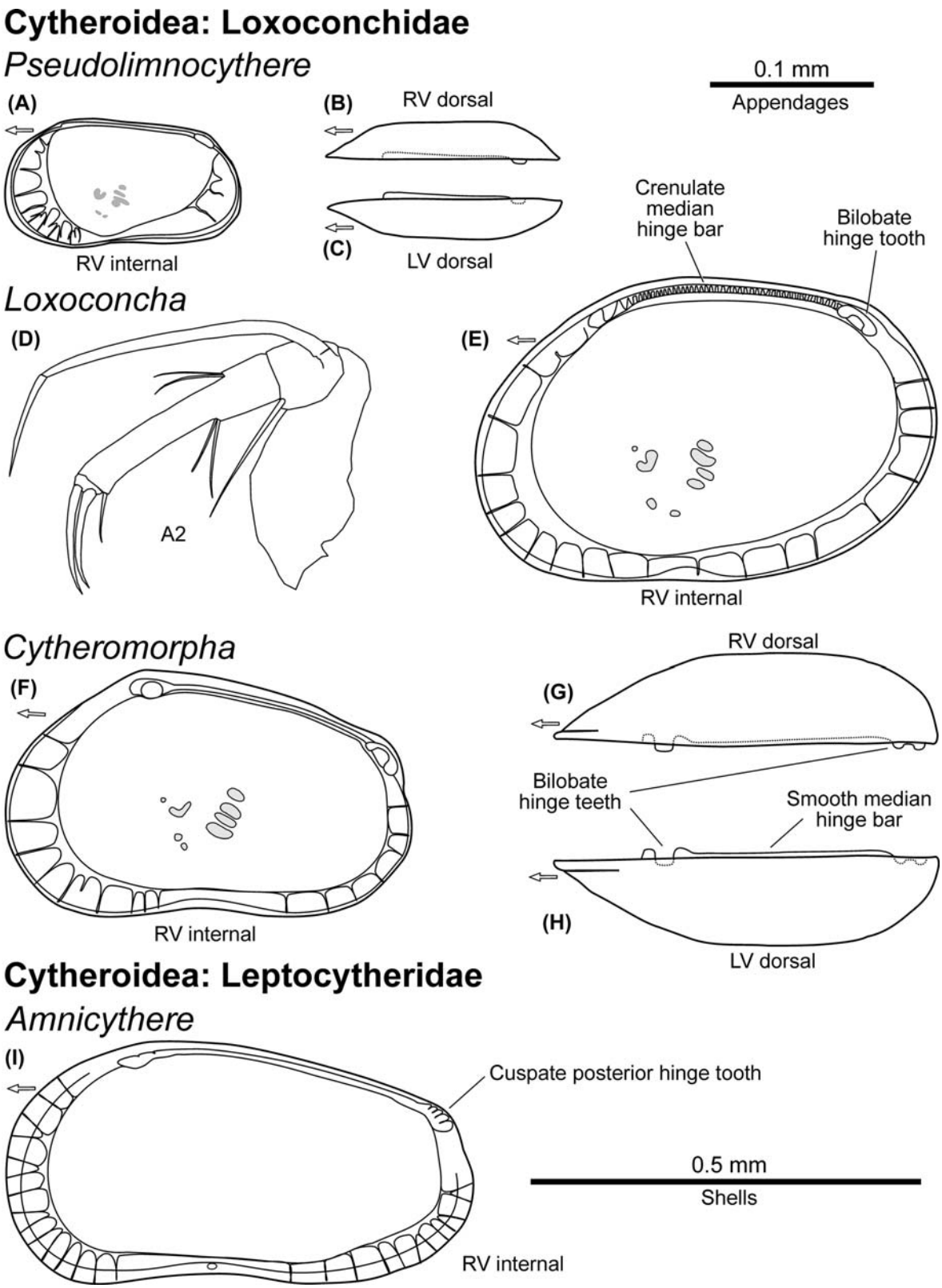


FIGURE 16.3.26 Key characteristics of genera of the Loxoconchidae and Leptocytheridae.

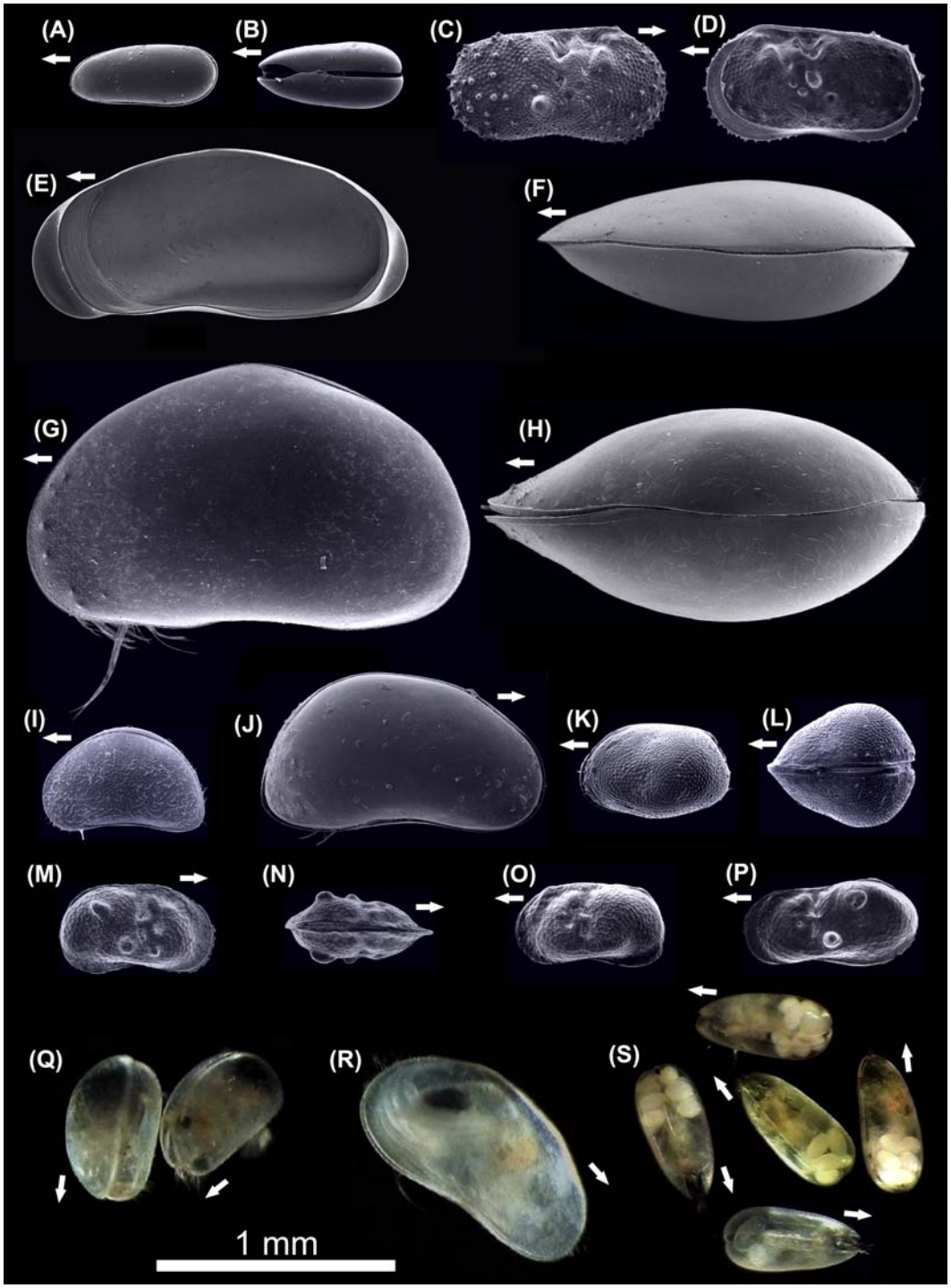


FIGURE 16.3.27 Scanning electron microscopy (A–P) and high resolution video microscopy (Q–S) images of freshwater ostracods. (A and B): *Darwinula*, adult female carapace left side (A) and ventral (B); (C and D): *Ilyocypris* adult female RV external: (C) and internal (D); (E and F): *Candonocypris*, adult female RV internal and carapace dorsal (F); (G and H): *Eucypris*, adult female carapace left side: (G) and dorsal (H); (I) *Potamocypris*, adult female carapace left side; (J) *Candona*, adult female carapace right side; (K and L): *Metacypris*, adult female carapace left side (K) and dorsal (L); (M–P): *Limnocythere*, tuberculate adult female RV external (M) and carapace dorsal (N), nontuberculate adult female LV external (O) and tuberculate male LV external (P); (Q): *Scottia*, two live adult females; (R) *Candonopsis*, live adult male; (S) *Darwinula*, five live adult females with eggs or juveniles in the brood chamber.

Ostracoda: Cytheroidea: Loxoconchidae: Genera

1	Hinge gongylodont (bilobate teeth anteriorly in LV and posteriorly in RV)	2
1′	Hinge henodont (single posterior tooth in RV) (Figs. 16.3.26 A–C)	*Pseudolimnocythere*
2(1)	RV median hinge bar crenulate (Figs. 16.3.26 D, E)	*Loxoconcha*
2′	RV median hinge bar smooth (Figs. 16.3.26 F–H)	*Cytheromorpha*

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Chapter 16.4

Arthropoda: Copepoda

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INTRODUCTION

More than 2814 copepod morphospecies inhabit fresh water. The Palaearctic has 1204 recorded species, more than double the number recorded for any other region (Boxshall & Defaye, 2008). Copepods have colonized many different habitats. Most are planktonic to benthic and may occur in ephemeral waterbodies, rock hollows, wet leaves, and mosses (Reid, 2001). Parasitic forms have the greatest taxa richness, as well as greatest family level diversity of any fish parasites.

LIMITATIONS

Copepod taxonomy and systematics are active areas of research. Palaearctic faunas of ephemeral, subterranean, interstitial, and semiterrestrial habitats are still poorly known, and new taxa are frequently being described. Moreover, taxonomic method refinements have led to redefinitions of many taxa, and more revisions are forthcoming. Investigators should consult with appropriate specialists and archive reference specimens. The parasitic taxa are poorly understood and are not considered here.

TERMINOLOGY AND MORPHOLOGY

Most Palaearctic free-living copepods do not exceed 0.3 mm in length and have various body shapes: elongated, fusiform, and cylindrical (Fig. 16.4.1). The number of apparent somites are variable between species, genera, and families, due to fusions between segments.

The largest groups are the Calanoida, Cyclopoida, and Harpacticoida. Calanoids are relatively large and have long first antennae, often as long as the body. They are usually planktonic and bear two egg sacs. The cyclopoid body is fusiform, and the first antenna has six to seventeen **antennomeres**, sometimes reaching beyond the

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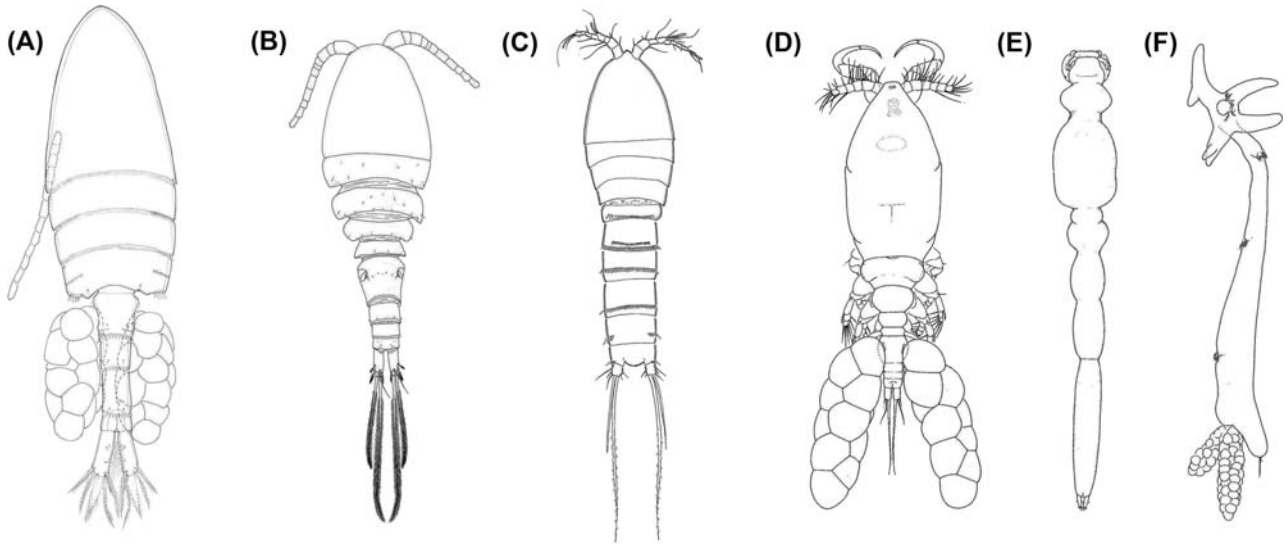


FIGURE 16.4.1 Common types of freshwater copepod: (A) Calanoida (*Pseudodiaptomus koreanus*); (B) Cyclopoida (*Monchenkocyclops changi*); (C) Harpacticoida (*Bryocamptus cheongokensis*); (D) Poecilostomatoida (*Neoergasilus angustus*); (E) Cyclopoida (*Lamproglena chinensis*); (F) Cyclopoida (*Lernaea cyprinacea*). *Figure from Soh et al., 2012 (A); Karanovic et al., 2012 (B); Lee & Lee, 2010 (C); Kim & Choi, 2003 (D–F).*

cephalosome. Most cyclopoids usually occur near hydrophytes or are planktonic, but some occur in sediment. Harpacticoids are mostly small, living interstitially, and generally have a cylindrical body type. The first antennae are short, with only six to nine antennomeres. Parasitic copepod bodies vary according to their host.

The body basically consists of a **prosome** and an **urosome** (Fig. 16.4.2). The prosome is composed of the **cephalosome** and the thoracic somites. The cephalosome contains the rostrum, first antennae, second antenna, and the mouth parts (mandible, first maxilla, second maxilla, and maxilliped). The posterior part of the body is the **urosome**, comprising the genital double somite (in females) and abdominal somites.

The swimming legs are **pereopods** (P1–P4) with an **exopodite** and an **endopodite**. The legs are fundamentally of three articles, but they may be reduced or even lost. In harpacticoids, the P1 endopodite apical article has a hooked or articulate seta depending on the species feeding mode and environment (Fig. 16.4.3).

The P5 is variable among copepod groups, and it has important taxonomic characters (number of setae and articles, shape) (Fig. 16.4.4). In male calanoids, the P5 **baseoendopod** is sometimes reduced or vestigial, or huge and asymmetrical. The female P5 may be of two types in some species (Fig. 16.4.4 B). In cyclopoids, the small P5 is held on the lateral abdominal surface. It is reduced with one to two articles without intercoxal sclerites. Harpacticoids have a simple P5, composed of the baseoendopodite and exopodite in both sexes.

MATERIAL PREPARATION AND PRESERVATION

Collecting methods vary. Planktonic species can be collected with a plankton net. Hand nets with a mesh size of 64 μm, or a small plankton net, are useful in small water bodies (pools and bogs, or amongst aquatic plants). Benthic species can be collected by grab or core samplers. Substrate sampling is also useful. Copepods can be collected from interstitial habitats by digging a hole in wet sandy soil and running the water from the hole through a plankton net. Copepods can be preserved in a 70%–75% ethanol or 10% solution of formalin. Pure ethanol (>99%) is used for DNA sequencing.

Copepods are divided from the debris using a teasing needle under a microscope. Dissection of specimens is required for identification. The dissection should be performed on a glass slide under microscope. The body is usually dissected according to each somite, which makes it easy to isolate each appendage (Fig. 16.4.5). Dissection pins fine enough for copepods are made from copper-coated tungsten wire (Fig. 16.4.6). Small insect pins can be used in the dissection of the larger copepods.

The dissected appendages (and whole body) of one copepod should be placed on one slide. The specific slide preparation method can vary. The sandwich method is recommended to easily set and rotate the specimen (Fig. 16.4.7). The mounting medium used is lactophenol. Permanent slide mounts need to be filled with lactophenol and sealed with transparent nail varnish.

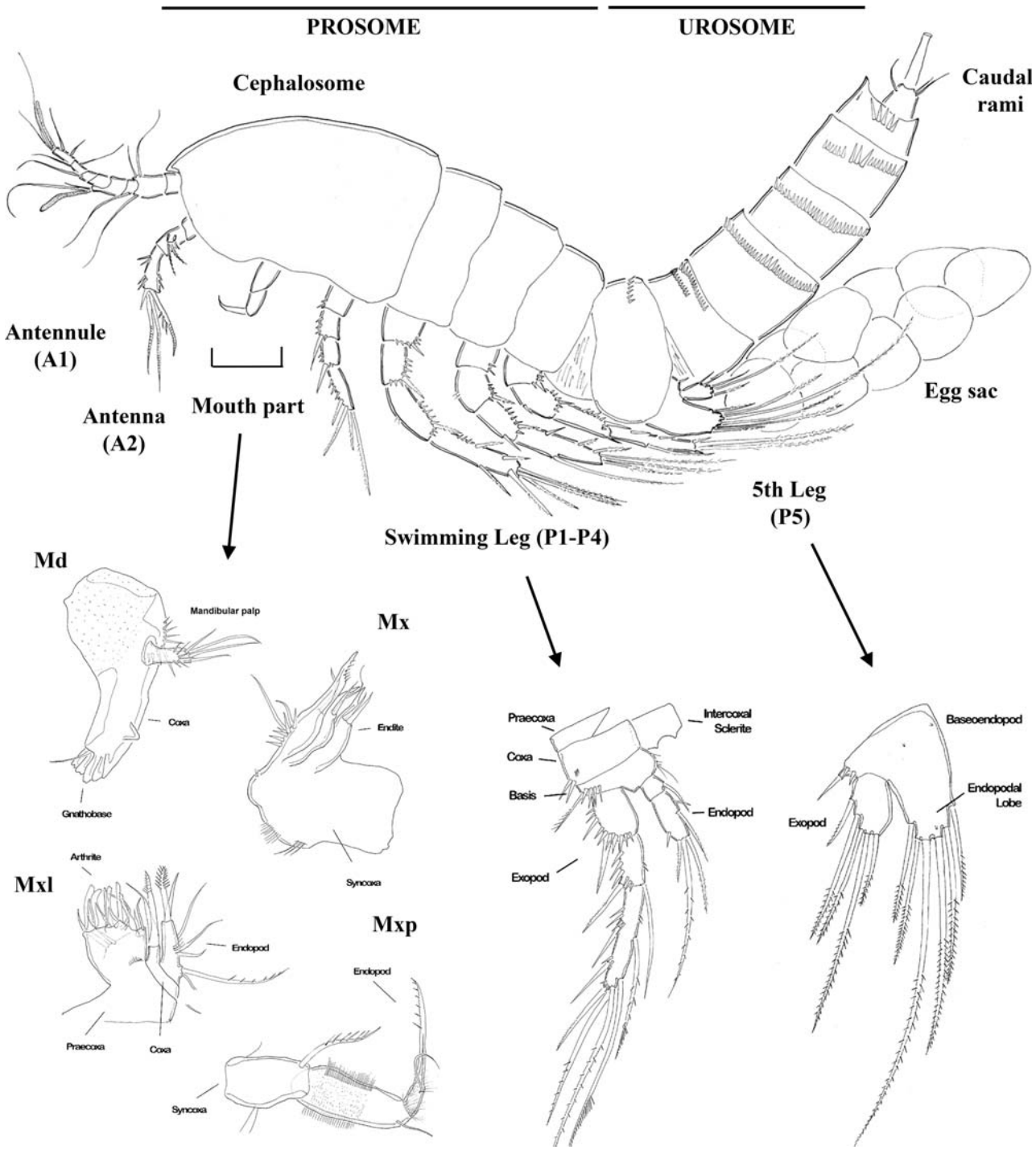


FIGURE 16.4.2 Structure of a copepod, mainly of a harpacticoid. *Md*, mandible; *Mx*, maxillule; *Mxl*, maxilla; *Mxp*, maxilliped. *Figures from Lee & Lee, 2010.*

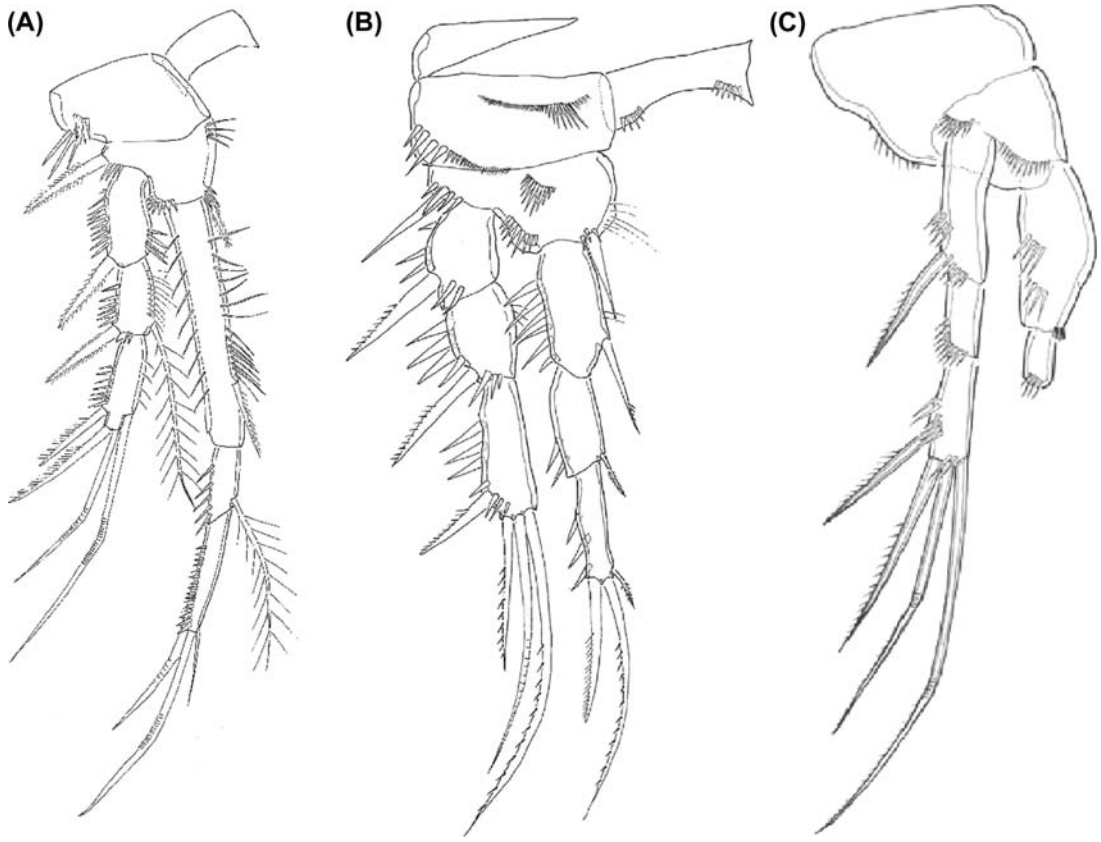


FIGURE 16.4.3 First leg (P1) of Harpacticoida: (A) *Canthocamptus* sp.; (B) *Bryocamptus cheongokensis*; (C) *Parastenocaris biwae*. *Not to scale. Figures from Lee & Lee, 2010 (B); Karanovic & Lee, 2012 (C).*

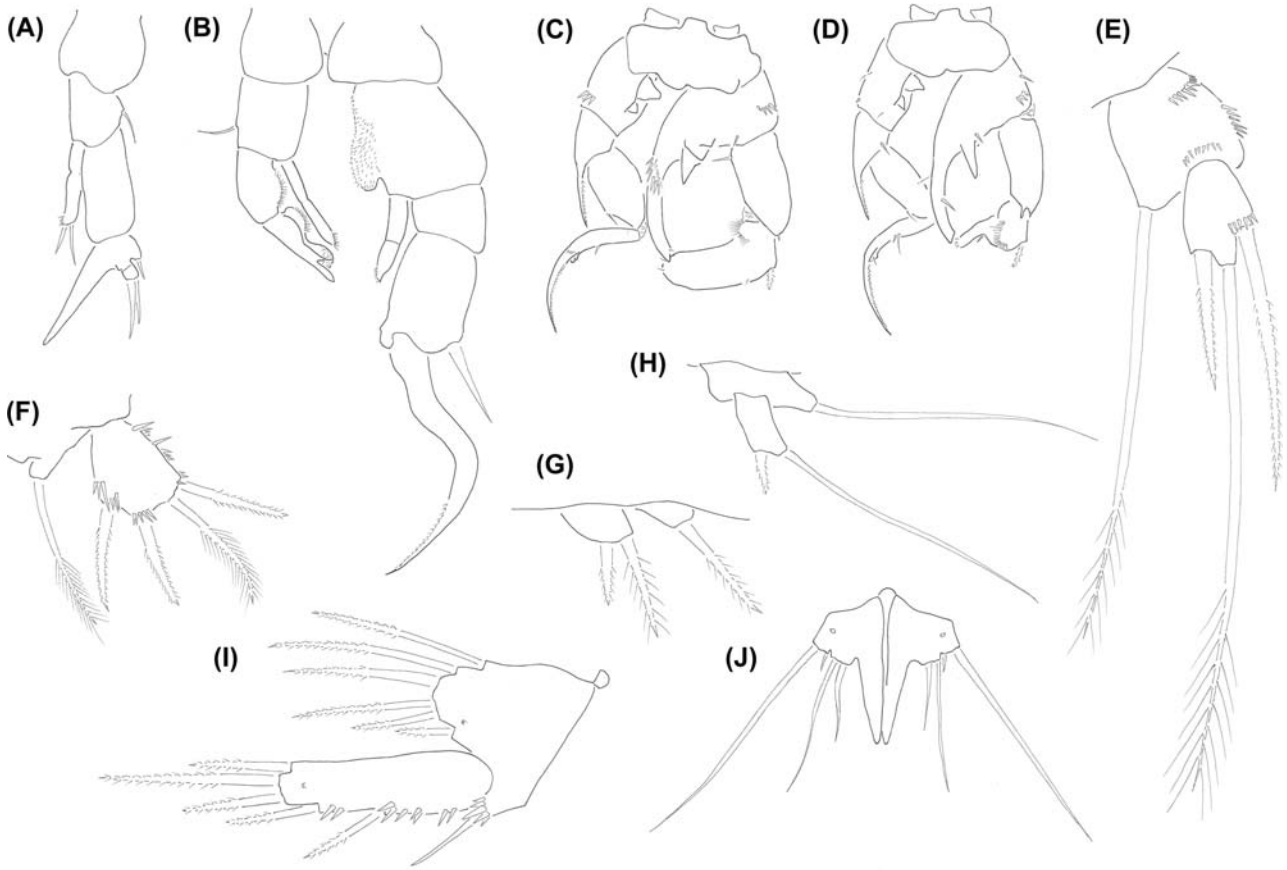


FIGURE 16.4.4 Various shape of fifth leg (P5) of freshwater copepods: Calanoida. *Hesperodiaptomus eiseni*, (A) female; (B) male; *Pseudodiaptomus inopinus*, male; (C) paddle type; (D) thumb type; Cyclopoida. (E) *Macrocyclops distinctus*; (F) *Halicyclops continentalis*; (G) *Speocyclops troglodyes*; (H) *Acanthocyclops sensitivus*; Harpacticoida. (I) *Canthocamptus* sp.; (J) *Parastenocaris biwae*. *Not to scale. Figures redrawn from Dussart & Defaye, 2001 (A and B); Chang, 2012 (E and G); Chang & Min, 2005 (F); Chappuis, 1923 (H); Karanovic & Lee, 2012 (J).*

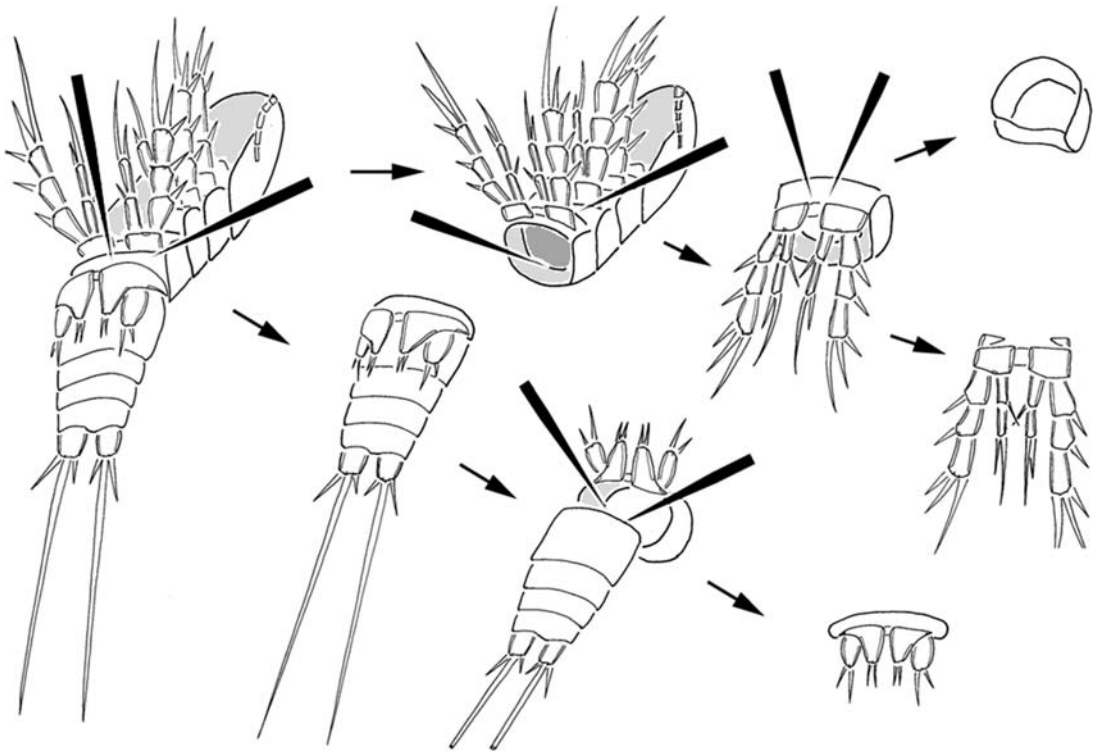


FIGURE 16.4.5 Dissection of copepod (Figures redrawn from T. Ito, 1970).

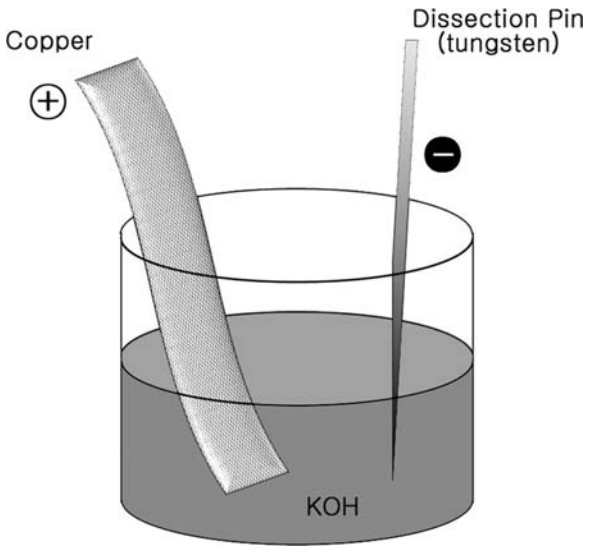


FIGURE 16.4.6 Method of making dissection pin.

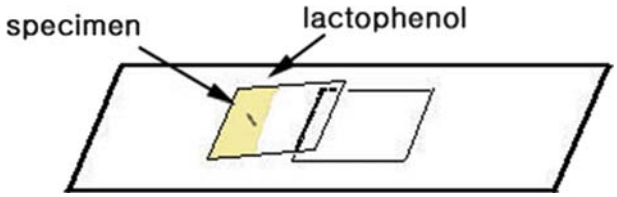


FIGURE 16.4.7 Sandwich method.

KEYS TO COPEPODA

Copepoda: Orders

The following keys present genus-level identifications for all free-living freshwater and estuarine Palaearctic copepod taxa. The Cyclopoid parasitic families Ergasilidae and Lernaeidae are not considered here. Important additional works include: Chang, 2009; Coulter, 1991; and Dussart & Defaye, 2001, 2006.

1	Body distinctly articulated between prosome and urosome 2
1′	No distinct articulation between prosome and urosome; pereopods 1–3 (P1–3) with coxa-basis completely fused; adult P5 absent; first antenna in both sexes geniculate ..... Gelyelloida, one family and genus: Gelyellidae, ***Gelyella*** **[p. 779]**
2(1)	Posterior part of the body, first somite with reduced legs; genital complex partly abdominal; both male first antennae geniculate or unmodified 3
2′	Posterior part of the body, first somite without appendages, followed by genital complex; male P5 prehensile; at most right first antenna geniculate ..... **Calanoida [p. 766]**
3(2)	Body cyclopiform; P5 (pereopod five) small, of 1–3 short articles, or represented only by setae, the basal article not enlarged medially ..... Cyclopoida, one family; **Cyclopidae [p. 770]**
3′	Body usually cylindrical; P5 broad, of 1–2 articles, basal article enlarged medially ..... **Harpactocoida [p. 774]**

Copepoda: Calanoida: Families

Calanoida is composed of 41 families (Razouls, 1995). Five families are present in the Palaearctic freshwater region.

1	Female with P5; all caudal setae similar 2
1′	Female without P5; male without geniculated first antennae; four long caudal setae are directed along the body axis, with the fifth (lateral most) oblique (Figs. 16.4.7 A, B) ..... Aetideidae, one species: *Senecella calanoides* Juday, 1923
2(1)	P1 to P4 with endopod of three articles; P5 asymmetrical in both sexes 3
2′	P1 to P4 with endopod of 1–3 articles 4
3(2)	P1 basis with medial seta absent; female P5 without endopod; male P5 with endopod uniarticulate ..... **Pseudodiaptomidae [p. 766]**
3′	P1 basis with medial seta present; female P5 typically of three articles; male P5 asymmetrical ..... **Centropagidae [p. 767]**
4(2)	P1 endopod of two articles, P2-P4 endopod of three articles ..... **Diaptomidae [p. 767]**
4′	P1–P4 endopod of one article OR P1 endopod of one article and P2–P4 endopod of two articles ..... **Temoridae [p. 770]**

Copeoda: Calanoida: Pseudodiaptomidae: Genera

A cosmopolitan genus of mostly estuarine species; may migrate into fresh water coastally.

1	First antennae with fewer than 25 antennomeres 2
1′	First antennae with 25 antennomeres; P5 without endopod; male right P5 with terminal claw directed laterally (Figs. 16.4.7 C, D) .... *Calanipeda*
2(1)	First antennae with 24 antennomeres ..... *Archidiaptomus*
2′	First antennae with 20–22 antennomeres ..... *Pseudodiaptomus*

Copepoda: Calanoida: Centropagedae

Marine, brackish, and freshwater species.

1	P1 exopod articles 1−2 lacking spines	2
1′	P1 exopod articles one and two each with lateral spine	*Boeckella*
2(1)	Antenna exopod with seven antennomeres, antennomeres 1 and 3−6 short in male	*Limnocalanus*
2′	Antenna exopod with six antennomeres, antennomeres 2−5 short in male	*Sinocalanus*

Copepoda: Calanoida: Diaptomidae: Subfamilies

1	P1 exopod of 2−3 articles; P2 to P4 with exopod and endopod of three articles	2
1′	P1−P3 exopod of two articles	3
2(1)	P1 exopod apical article with two marginal lateral spines; male right first antennae with three antennomeres behind geniculation (Figs. 16.4.8 E, F, K−M)	Paradiatominae, one species: *Neolovenula alluaudi* Guerne & Richard, 1980
2′	P1 exopod apical article with one marginal lateral spine; male right first antennae with four antennomeres behind geniculation	**Diaptominae [p. 768]**

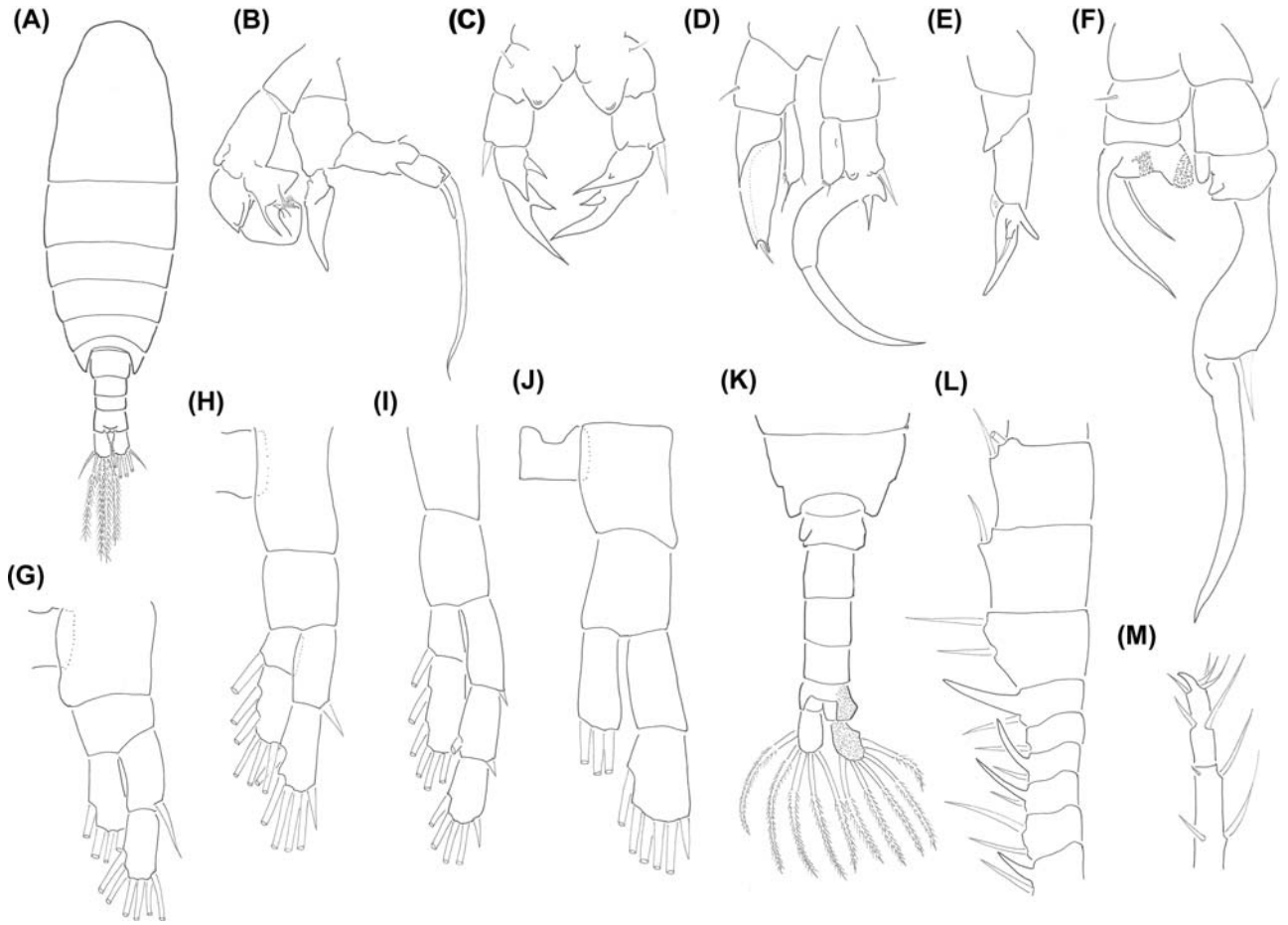


FIGURE 16.4.8 Representative structure of calanoid copepods: (A) *Senecella calanoides* male habitus; (B) *S. calanoides* male P5; (C) *Calanipeda aquaedulcis* female P5; (D) *C. aquaedulcis* male P5; (E) *Neolovenula alluaudi* female P5; (F) *N. alluaudi* male P5; (G) *Speodiaptomus birsteini* male P1; (H) *S. birsteini* male P2; (I) *S. birsteini* male P4; (J) *Troglodiaptomus sketi* male P4; (K) *N. alluaudi* female urosome; (L) *N. alluaudi*, antennulal segment 8−16; (M) *N. alluaudi*, antennule terminal segment. *Not to scale. Figures redrawn from Dussart & Defaye, 2001 (A, B, E, F, and K−M); Dussart, 1990 (C and D); Kiefer, 1978 (G−I); Petkovski, 1978 (J).*

3(1)	P4 exopod of three articles; P1 endopod unarticulate; P2–P4 endopod of two articles (Figs. 16.4.8 G–I) ..... Speodiaptominae, one species: *Speodiaptomus birsteini* Borutsky, 1962	
3′	P4 exopod of two articles (Fig. 16.4.8 J); P1–P4 endopod of unarticulate ..... Microdiaptominae, one genus: *Troglodiaptomus*	

Copepoda: Calanoida: Diaptomidae: Diaptominae: Genera

1	Thoracic somites glabrous	2
1′	Some thoracic somites with posterior edge ornamented with filiform setae (Figs. 16.4.9 A–D)	*Eodiaptomus*
2(1)	Male right first antennae with antennomeres 13 to 19 dilated and bearing a spiniform process, at least on antennomere 13	3
2′	Male right first antennae with antennomeres 13 to 19 undilated	*Spelaeodiaptomus*
3(2)	P1 first exopod with a lateral spine	4
3′	P1 first exopod without lateral spine; P1–P4 second endopod medial margin with a single seta	*Stygodiaptomus*
4(3)	Female last thoracic somite without hump	5
4′	Female last thoracic somite dorsally humped; male right P5 endopod reaching posterior edge of first exopod; male left P5 second exopod ending in a lamella (Figs. 16.4.9 I, J)	*Sinodiaptomus*

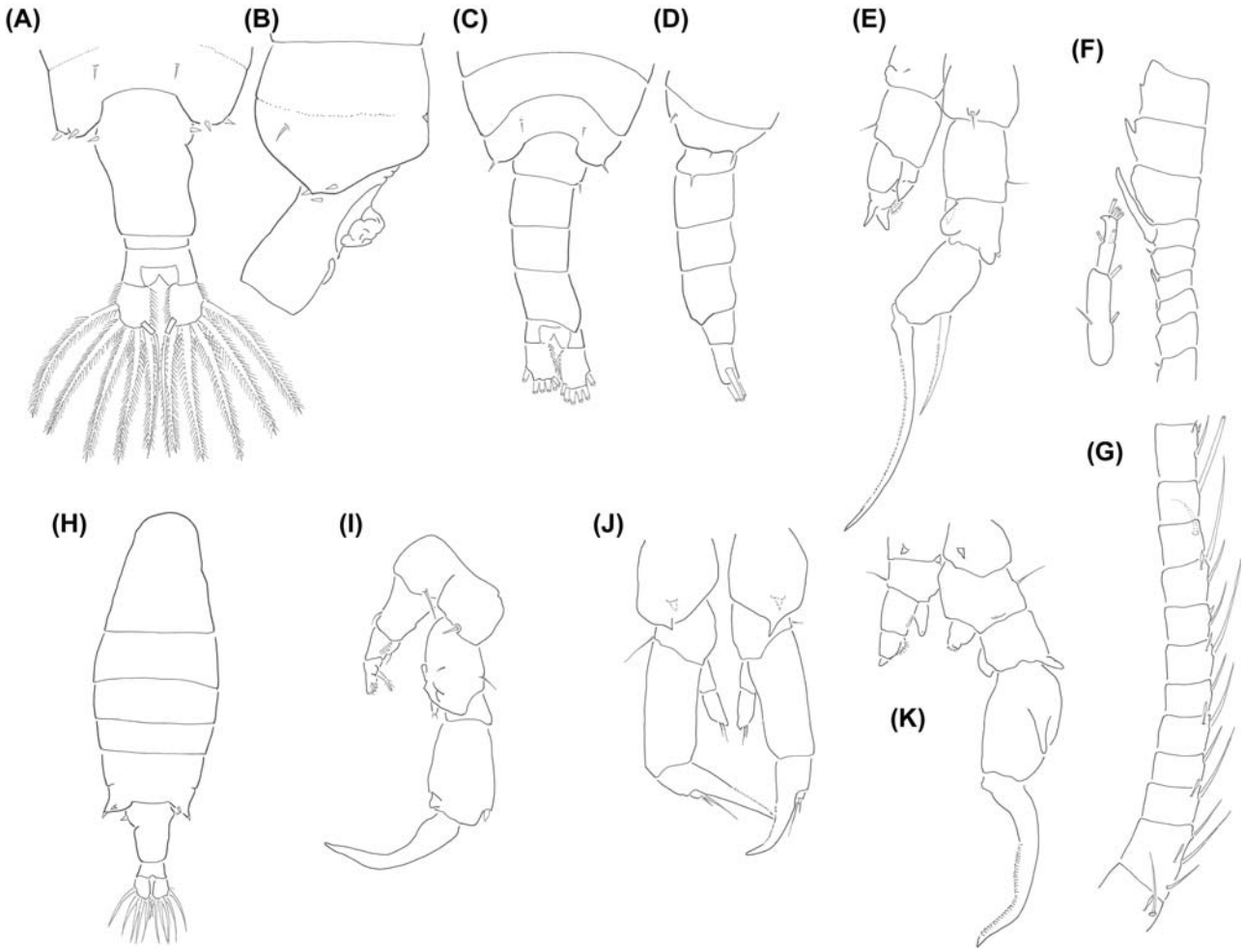


FIGURE 16.4.9 Representative structure of calanoid copepods: (A) *Eodiaptomus lumholtzi* female last thorax segment and urosome, dorsal; (B) *E. lumholtzi* female last thorax segment and genital field, lateral; (C) *E. lumholtzi* male last thorax and urosome, dorsal; (D) *E. lumholtzi* male last thorax and urosome, lateral; (E) *Acanthodiaptomus denticornis* male P5; (F) *A denticornis* male A1; (G) *A. denticornis* female A1; (H) *Sinodiaptomus sarsi* female habitus; (I) *S. sarsi* male P5; (J) *Ligulodiaptomus linhuensis* female P5; (K) *L. linhuensis* male P5. *Not to scale. Figures redrawn from Ranga Reddy & Dumont, 1998 (A–D); Kiefer, 1978 (E–G); Dussart & Defaye, 2001 (H and I); Shen & Tai, 1962 (J and K).*

5(4)	Male right P5 not as below 6
5′	Male right P5 second exopod cylindrical and bearing a short, broad-based, linguiform aculeus (Figs. 16.4.9 K, L) ..... *Ligulodiaptomus*
6(5)	Male right first antenna without terminal armature (other than setae) 7
6′	Male right first antenna, antennomere 13 bearing a very long spiniform extension, and last antennomere with a small falciform extension; Male left P5 second exopod lateral surface with a seta (Figs. 16.4.8 E–H) ..... *Acanthodiaptomus*
7(6)	Male left P5 exopod of 2–3 articles 8
7′	Male left P5 exopod unarticulate, with apex spatulate ..... *Tropodiaptomus*
8(7)	Male left P5 exopod of two articles 9
8′	Male left P5 exopod of three articles ..... *Onychodiaptomus*
9(8)	Male right first antenna antepenultimate antennomere with large distal process 10
9′	Male right first antenna antepenultimate antennomere with at most a narrow hyaline lamella 21
10(9)	Male right first antenna antepenultimate antennomere with a bacilliform or hooked process 11
10′	Male right first antenna antepenultimate antennomere with a pectinate process (Fig. 16.4.10 A) ..... *Arctodiaptomus*
11(10)	Male right first antenna antepenultimate antennomere with a hooked process 12
11′	Male right first antenna antepenultimate antennomere with a bacilliform, more or less elongate, digitiform process ..... *Mongolodiaptomus*
12(11)	Male right first antenna antepenultimate antennomere with a short, hooked process 13
12′	Male right first antenna antepenultimate antennomere with hooked process elongate and/or curved, longer than apical antennomere (Fig. 16.4.9 B) ..... *Hesperodiaptomus*

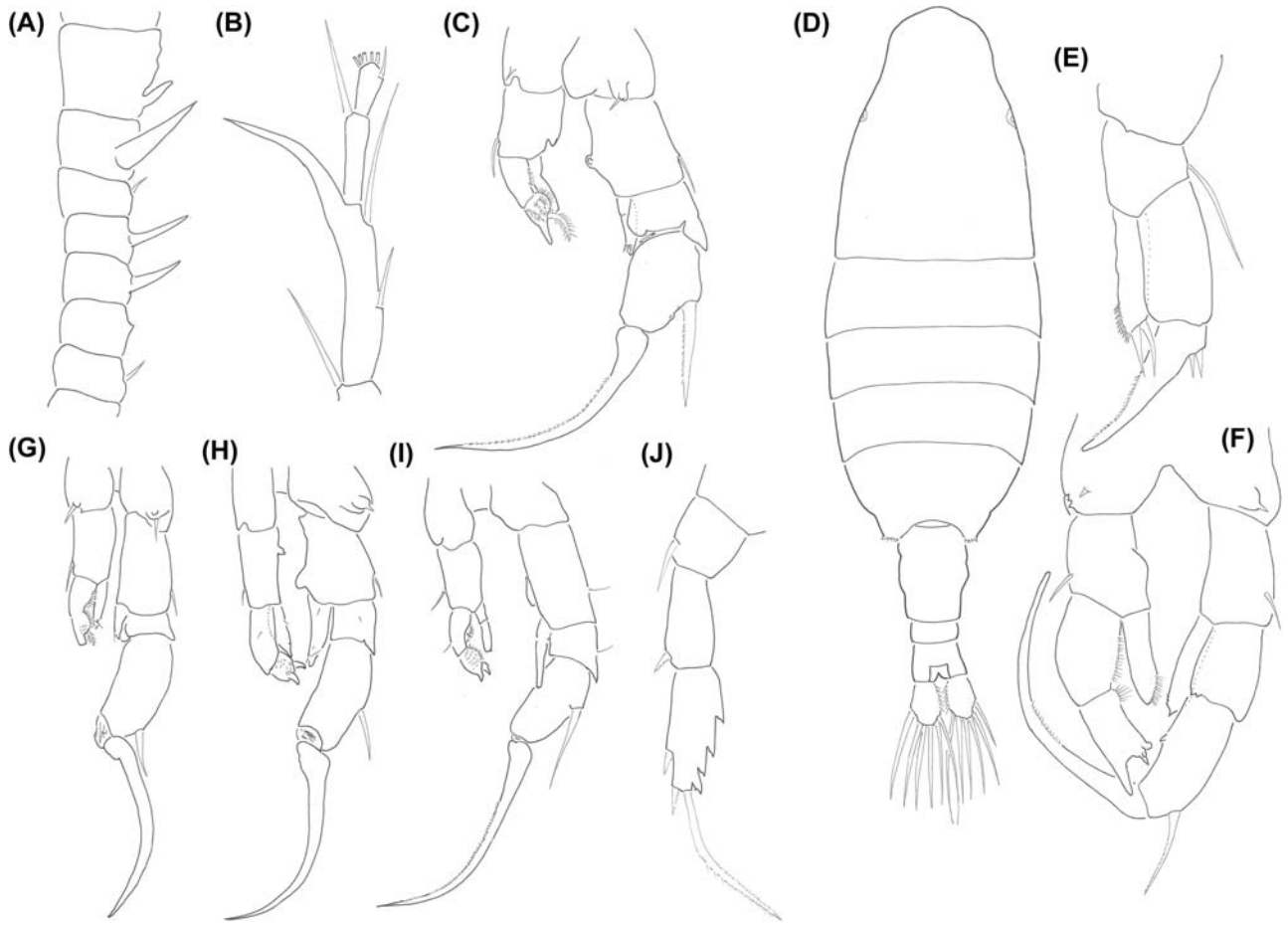


FIGURE 16.4.10 Representative structure of calanoid copepods: (A) *Arctodiaptomus wierzejskii* male A1; (B) *Hesperodiaptomus eiseni* apical segment of male A1; (C) *Eudiaptomus vulgaris* male P5; (D) *Skistodiaptomus oregonensis* female habitus; (E) *S. oregonensis* female P5; (F) *S. oregonensis* male P5; (G) *Copidodiaptomus stueri* male P5; (H) *Mixodiaptomus kupelwieseri* male P5; (I) *Diaptomus castor* male P5; (J) *Heterocope borealis* female P5. *Not to scale. Figures redrawn from Kiefer, 1978 (A, C, G, and J); Dussart & Defaye, 2001 (B and D–F).*

13(12)	Female P5 endopod ending in two setae and a more or less oblique row of filiform setae	14
13′	Female P5 endopod ending only in a more or less oblique row of filiform setae	20
14(13)	Male left P5 second exopod with lateral seta short, not overlapping the article of origin	15
14′	Male left P5 second exopod with lateral seta very long; left first antenna with antennomeres 17, 19, 20, and 22 with setae ending in a spine	*Aglaodiaptomus*
15(14)	First antenna with antennomere 11 with two setae in female and in male left side only	16
15′	First antenna with antennomere 11 bearing one seta in female and in male left side only	18
16(15)	Male left P5 with second exopod shorter than first exopod	17
16′	Male left P5 with second exopod longer than first exopod	*Hemidiaptomus*
17(16)	Male right P5 second exopod proximally with a short aculeus; female genital segment generally asymmetrical	*Neutrodiaptomus*
17′	Male right P5 second exopod aculeus at least as long as exopod width, inserted on the middle or distal half of exopod (Fig. 16.4.10 I)	*Diaptomus*
18(15)	Male left P5 second exopod shorter than first exopod, digitiform distally	19
18′	Male left P5 second exopod shorter than first exopod, digitiform distally with short and obtuse lateral setae	*Leptodiaptomus*
19(15)	Male left P5 second exopod with lateral seta curved, plumose and well developed (Fig. 16.4.10 C)	*Eudiaptomus*
19′	Male left P5 second exopod with lateral seta weakly developed, and with a small spine basally (Figs. 16.4.10 D–F)	*Skistodiaptomus*
20(13)	Male left P5 ending in a thick digitiform process flanked by a pennate seta of the same size or smaller (Fig. 16.4.10 G)	*Copidodiaptomus*
20′	Male left P5 extremity short, blunt, flanked by a spiniform seta; male left P5 second exopod with lateral seta curved, short, thick (Fig. 16.4.10 H)	*Mixodiaptomus*
21(9)	Female P5 third exopod with two short, subequal spines; male caudal rami without special ornamentation	*Nordodiaptomus*
21′	Female P5 third exopod with two unequal spines; male left caudal ramus with a dentiform process at distomedial corner	*Odontodiaptomus*

Copepoda: Calanoida: Temoridae: Genera

1	P3 and P4 endopod unarticulated	2
1′	P3 and P4 endopod of two articles; P1 endopod unarticulated	*Eurytemora*
2(1)	Female P5 with distal article serrate (Fig. 16.4.10 J)	*Heterocope*
2′	Female P5 not serrate	*Epischura*

Copepoda: Cyclopoida: Cyclopidae: Subfamilies

The Cyclopidae is the large freshwater family, which comprises over 800 species (Dussart & Defaye, 2006).

1	Female P5 apical segment with 2 or 3 setae	2
1′	Female P5 apical segment with four setae	**Haicyclopinae [p. 770]**
2(1)	Female P5 apical segment with three setae, last prosome somite with spinules	**Eucyclopinae [p. 771]**
2′	Female P5 apical segment with two setae, last prosome somite without spinules	**Cyclopinae [p. 771]**

Copepoda: Cyclopoida: Cyclopidae: Haicyclopinae Genera

1	Maxilliped normal or reduced	2
1′	Maxilliped absent (Figs. 16.4.11 A, B)	*Colpocyclops*
2(1)	Maxilliped and other oral appendages normally developed	3
2′	Maxilliped one article with a seta	*Smirnoviella*
3(2)	P5 of three articles (Fig. 16.4.11 C); female first antennae with 8–12 antennomeres	*Neocyclops*
3′	P5 of two articles (Fig. 16.4.11 D); female first antennae with six antennomeres	*Halicyclops*

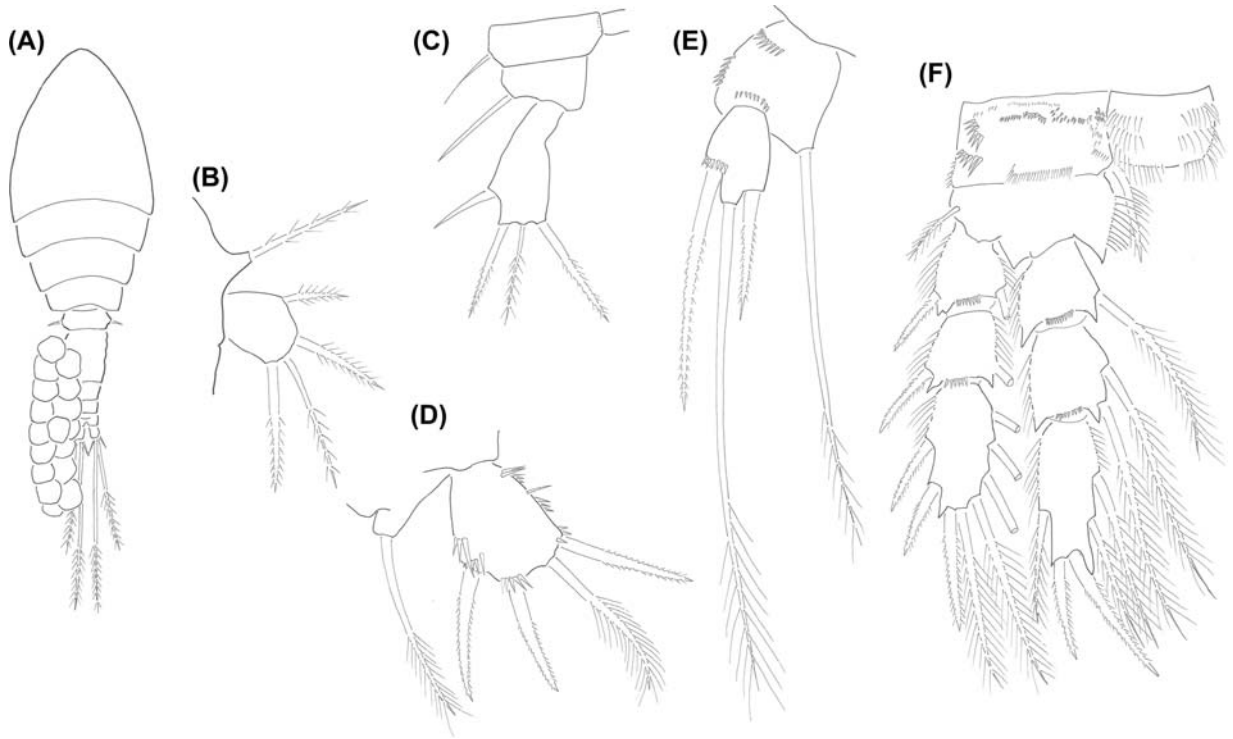


FIGURE 16.4.11 Representative structures of cyclopoid copepods: (A) *Colpocyclops dulcis* female habitus; (B) *C. dulcis* female P5; (C) *Neocyclops salinarum* female P5; (D) *Halicyclops continentalis* female P5; (E) *Macrocyclops distinctus* female P5; (F) *Eucyclops roseus* female P4. *Not to scale. Figures redrawn from Monchenko, 1977 (A and B); Dussart, 1969 (C); Chang, 2012 (D); Chang & Min, 2005 (E and F).*

Copepoda: Cyclopoida: Cyclopidae: Eucyclopinae: Genera

1	P5 unarticulated, more or less completely fused to the fifth thoracic somite	2
1′	P5 of two articles (Fig. 16.4.11 E), apical article with two spines and one seta	*Macrocyclops*
2(1)	P4 basioendopod with medial angle rounded	3
2′	P4 basioendopod with medial angle sharply produced (Fig. 16.4.11 F)	*Eucyclops*
3(2)	Seminal receptacle with anterior part not as below	4
3′	Seminal receptacle with anterior part tapering laterally as distorted horns	*Tropocyclops*
4(3)	P5 unarticluated, with one medial spine and two setae; caudal rami smooth or with only a more or less transversal row of spinules	5
4′	P5 fused to fifth thoracic somite and represented by three spiniform setae (Fig. 16.4.12 B); caudal rami ornamented with several rows of transverse spinules (Fig. 16.4.12 A)	*Ectocyclops*
5(4)	Caudal rami with a row of spinules (Fig. 16.4.12 D); P5 with an apical spine, a lateral seta and a medial spine (Fig. 16.4.12 C)	*Paracyclops*
5′	Caudal rami smooth; P5 with three appendages inserted apically (Figs. 16.4.12 F, G)	*Ochridacyclops*

Copepoda: Cyclopoida: Cyclopidae: Cyclopinae*:* Genera

1	P5 1−3 articles	2
1′	P5 fused to fifth thoracic somite	3
2(1)	P5 of 1−2 articles	6
2′	P5 with three articles (Fig. 16.4.12 E)	*Orthocyclops*
3(1)	P4 coxa without medial seta	4

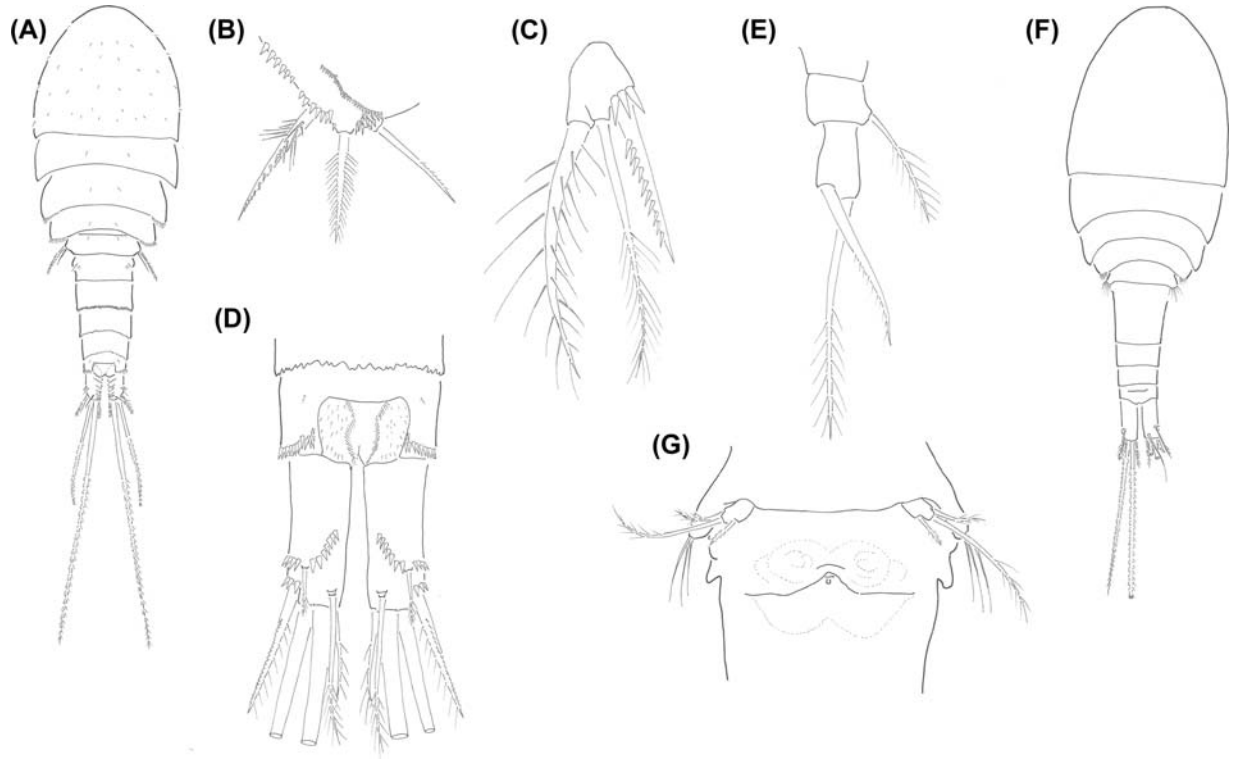


FIGURE 16.4.12 Representative structures of cyclopoid copepods: (A) *Ectocyclops phlaeratus* female habitus; (B) *E. phlaeratus* female P5; (C) *Paracyclops fimbriatus* female P5; (D) *P. fimbriatus* caudal rami; (E) *Orthocyclops modestus* female P5; (F) *Ochridacyclops coreensis* female habitus; (G) *O. coreensis* female P5 and genital field. *Not to scale. Figures redrawn from Chang & Min 2005 (A–D); Dussart & Defaye, 2001 (E); Herrick, 1883 (G).*

3′	P4 coxa with a medial seta	*Allocyclop/Hypocyclops*
4(3)	P1 exopod with three spines	5
4′	P1 exopod with two spines	*Graeteriella*
5(4)	P1–P4 exopod with spine formula 2.3.3.3 and seta formula 5.5.5.4; anal operculum produced and triangular (Figs. 16.4.13 A–C)	*Palaeocyclops*
5′	P1–P4 exopod with spine formula 2.3.3.3 and seta formula 5.4.4.4; anal operculum quadrate and not produced	*Stolonicyclops*
6(2)	P5 unarticulated	7
6′	P5 of two articles	12
7(6)	P5 free article narrow, or only slightly longer than wide, its apicomedial spine or seta (if present) inserted near apicolateral spine	8
7′	P5 free article broad, its apicomedial spine inserted far from the apicolateral seta (Fig. 16.4.13 D)	*Apocyclops*
8(7)	P5 free article only slightly longer than wide	9
8′	P5 free article narrow, cylindrical with medial spine tiny, inserted subterminally or medially	10
9(8)	P5 free article with two elements	11
9′	P5 free article with a long seta	*Idiocyclops*
10(9)	P5 free article with stout apicomedial spine and apicolateral seta both inserted terminally, subterminally, or medially	*Metacyclops*
10′	P5 free article as long as wide, with stout apicomedial seta or spine inserted next to apicolateral seta, and subequal in length	*Itocyclops*
11(9)	P1–P4 intercoxal sclerites and coxa-basis 2.5 x wider than long; P2–P4 basis medial expansion with rows of spinulae; P4 endopod apicolateral spine less than 1/6 length of apicomedial spine	*Cryptocyclops*
11′	P1–P4 intercoxal sclerites and coxa-basis 2.0 x wider than long; P2–P4 basis medial expansion with fine setae; P4 endopod apicolateral spine at least 1/2 length of apicomedial spine	*Microcyclops*
12(6)	P5 terminal article depending from first article	13
12′	P5 articles placed side by side (Fig. 16.4.13 E)	*Speocyclops*
13(12)	P5 distal article bearing one apical seta and a medial marginal or subapical spine more than 4 x length of article	14

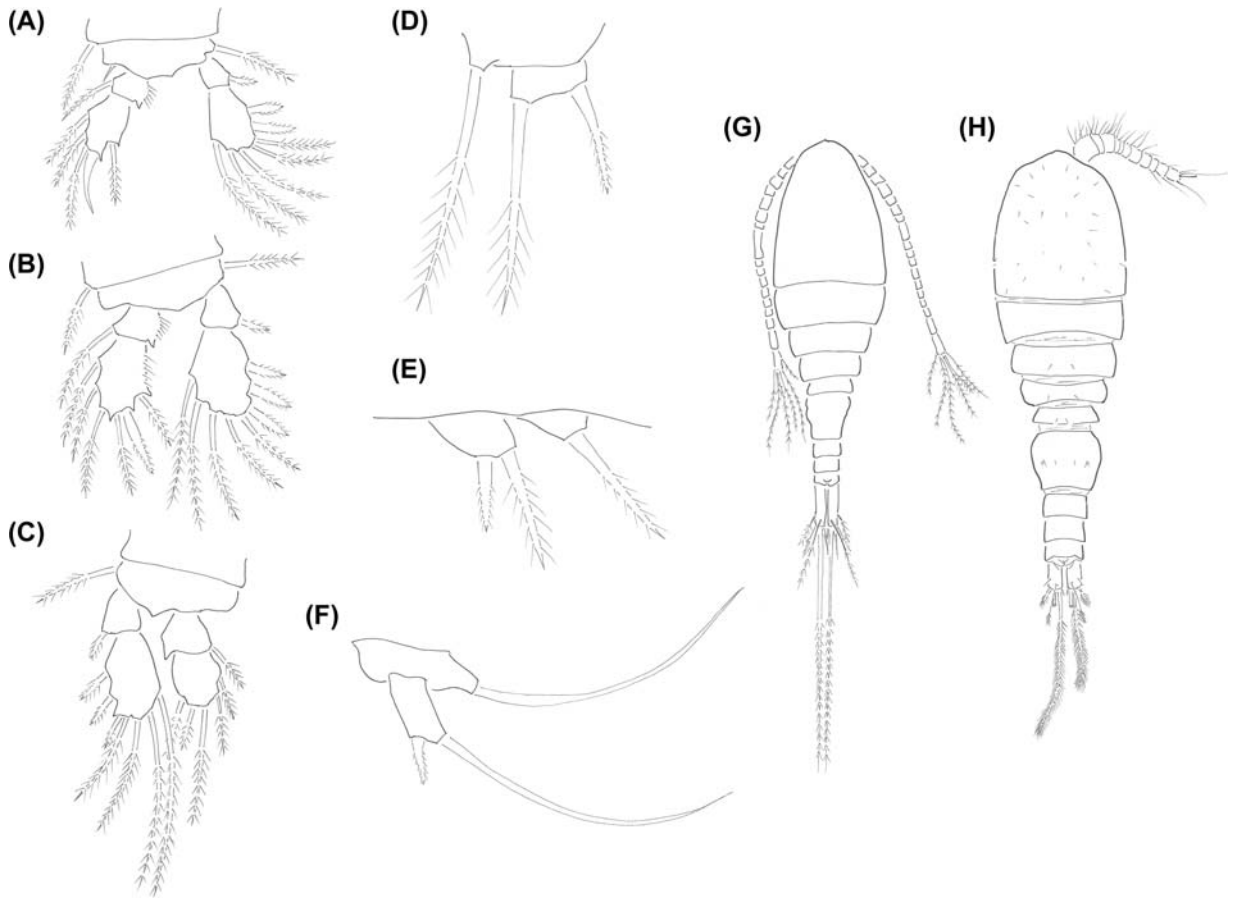


FIGURE 16.4.13 Representative structures of cyclopoid copepods: (A) *Palaeocyclops jankowskajae* female P1; (B) *P. jankowskajae* female P3; (C) *P. jankowskajae* female P4; (D) *Apocyclops dengizicus* female P5; (E) *Speocyclops troglodytes* female P5; (F) *Acanthocyclops sensitivus* female P5; (G) *Kieferiella delamarei* female habitus; (H) *Diacyclops hankuk* female habitus. *Not to scale. Figures redrawn from Monchenko, 1972 (A–C); Monchenko, 2003 (D); Chappuis, 1923 (E); Chang, 2009 (F) Lescher-Moutoué, 1971 (G); Karanovic, Grygier & Lee, 2013 (H).*

13′	P5 distal article bearing one apical seta and a medial marginal or subapical spine not more than twice length of article	15
14(13)	P5 distal article medial spine inserted about midlength on margin	*Mesocyclops*
14′	P5 distal article medial spine inserted subterminally	*Thermocyclops*
15(13)	P5 distal article with an apical seta and a small slender subapical medial spine	16
15′	P5 distal article with an apical seta and a large medial, marginal spine	*Cyclops*
16(15)	P5 second article with an apical seta and a small medial spine or spur	17
16′	P5 second article with a medial subapical spine longer than article	19
17(16)	P5 second article with an apical seta and small spine or spur	18
17′	P5 second article with an apical seta and small spine slightly distad of middle, or subapical (Fig. 16.4.13 F)	*Acanthocyclops*
18(17)	Caudal ramus with medial surface hirsute	*Megacyclops*
18′	Caudal ramus without medial surface hirsute	*Monchenkocyclops*
19(16)	First antennae very long, reaching genital article (Fig. 16.4.13 G)	*Kieferiella*, one species: *Kieferiella delamarei* Lescher-Moutoué, 1971
19′	First antennae short, seminal receptable variable, but never malleoform (Fig. 16.4.13 H)	*Diacyclops*

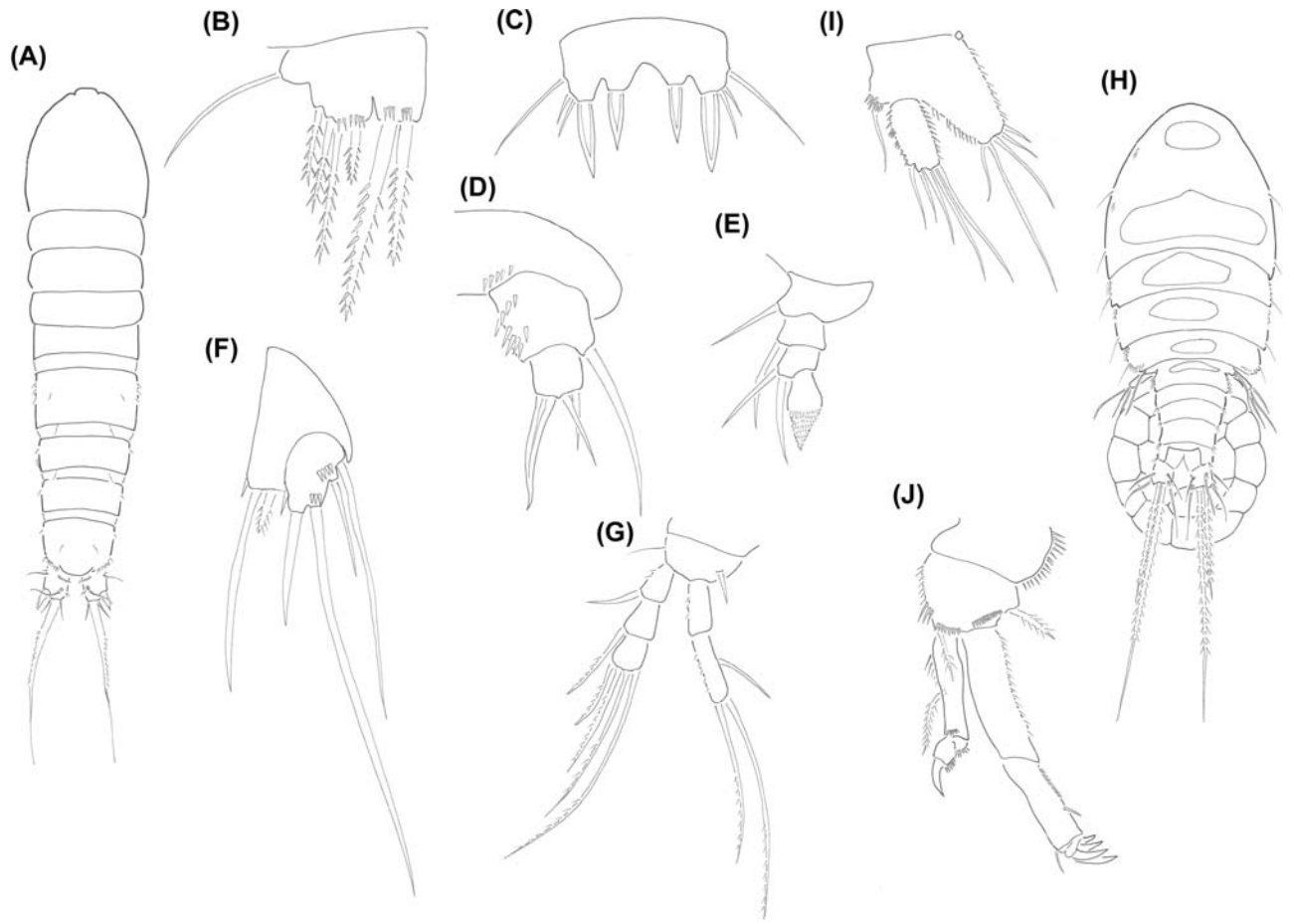


FIGURE 16.4.14 Representative structures of harpacticoid copepods: (A) *Phyllognathopus viguieri* female habitus; (B) *P. viguieri* female P5; (C) *Chappuisius inopinus* female P5; (D) *C. inopinus* male P5; (E) *Chappuisius singeri* male P5; (F) *Ectinosoma soyeri* female P5; (G) *C. inopinus* female P1; (H) *Harpacticiella paradoxa* female habitus; (I) *H. paradoxa* female P5; (J) *H. paradoxa* female P1. *Not to scale. Figures redrawn from Chang, 2009 (A and B); Kiefer, 1938 (C and G); & Boxshall, 1991 (D); Chappuis, 1940 (E); Apostolov, 1975 (F); Chang, 2009 (H–J).*

Copepoda: Harpacticoida: Families

Mostly benthic including temporary water bodies (moss, phytotelmata), phreatic habitats and wet soils.

1	Cephalosome free, not fused with first pedigerous somite to form cephalothorax	2
1′	Cephalosome and first pedigerous somite fused to form cephalothorax	3
2(1)	Antenna exopod unarticulate; P2 to P4 endopods with 2–3 articles (Fig. 16.4.14 A, B)	Phyllognathopodidae, one genus: *Phyllognathopus*
2′	Antenna exopod with two articles; P2 to P4 endopods with one article	**Chappuisiidae [p. 775]**
3(1)	Body variable, not fusiform; endopod 1 to 3 typically of three articles; P1 biramous, joined by intercoxal sclerite	4
3′	Body fusiform	**Ectinosomatidae [p. 775]**
4(3)	P1 not as below	5
4′	P1 exopod longer than endopod and typically of two articles with elongate second article bearing vestigial third article embedded apically and bearing 4 or 5 claws (Fig. 16.4.14 H–J)	Harpacticidae, one genus: *Harpacticella*
5(4)	P1 endopod elongate, prehensile, typically with first endopod as long as or longer than exopod	6
5′	P1 not as above; P2 to P4 endopods lacking or with 1–2 articles	9
6(5)	P1 basis medial spine not sexually dimorphic	7
6′	P1 basis medial spine sexually dimorphic	**Ameiridae [p. 775]**
7(6)	Not with the below combination of characters; eggs typically in single ventral mass	8

7′	P1 endopod distal article armed with a lateral claw, geniculate setae and small medial setae; eggs typically in paired egg sacs	Miraciidae
8(7)	P1 endopod distal article armed with a robust nongeniculate lateral claw and medial seta	Laophontidae
8′	P1 endopod distal article armed with a geniculate setae and small medial seta	**Canthocamptidae [p. 775]**
9(5)	P2 to P4 endopods typically with two articles; P3 not sexually dimorphic	10
9′	P2 to P4 endopods typically with one article; P3 sexually dimorphic, male leg highly modified, exopod often massive	**Parastenocarididae [p. 778]**
10(9)	P5 well developed with a separate exopod	Cletodidiae
10′	P5 very small and inconspicuous, with exopod and baseoendopod fused	Darcythompsoniidae, one genus: ***Leptocaris* [p. 779]**

Copepoda: Harpacticoida: Chappuisiidae: Species

1	P1 endopod distal article with four setae; male P5 baseoendopod of three articles (Fig. 16.4.14 E)	*Chappuisius singeri* Chappuis, 1940
1′	P1 endopod distal article with three setae (Fig. 16.4.14 F), male P5 baseoendopod of three articles (Fig. 16.4.14 D)	*Chappuisius inopinus* Kiefer, 1938

Copepoda: Harpacticoida: Ectinosomatidae: Genera

Mainly marine, but with a few estuarine and freshwater species.

1	Body fusiform, cephalothorax narrowed anteriorly	2
1′	Body cylindrical, cephalothorax rectangular, last somite with spiniform or unguiform structure	*Arenosetella*
2(1)	P1 endopod of three articles	3
2′	P1 endopod of two articles	*Pseudectinosoma*
3(2)	P5 exopod with three marginal setae	4
3′	P5 exopod with four marginal setae	*Ectinosoma*
4(3)	Maxilla endopod with two articles	*Pseudobradya*
4′	Maxilla endopod with at most one article	*Halectinosoma*

Copepoda: Harpacticoida: Ameiridae: Genera

Ameridae is especially diverse in subterranean waters (Rouch, 1986; Galassi, 2001), with 97 species in fresh water (Boxshall & Defaye, 2008). It is dominated by the genera *Nitokra* and *Nitocrella*. These genera inhabit karstic habitats, calcrete formations, and other subterranean waters.

1	Female P4 endopod free, unarticulate, or with endopod absent or reduced to a vestigial knob	2
1′	Female P4 endopod of 2–3 articles	4
2(1)	Female P1 second exopod with a lateral spine	3
2′	Female P1 second exopod lacking lateral spine	*Psammonitocrella*
3(2)	Female P4 endopod of one article, bearing single apical seta	*Stygonitocrella*
3′	Female P4 endopod vestigial, represented by minute, unarmed knob (Fig. 16.4.15 A, B)	*Neonitocrella*, one species: *Neonitocrella insularis* Miura, 1962
4(1)	Female P4 endopod of two articles	5
4′	Female P4 endopod of three articles	*Nitokra*
5(4)	Female P2 and P3 endopods of three articles	*Nitocrellopsis*
5′	Female P2 and P3 endopods of two articles	*Nitocrella*

Copepoda: Harpacticoida: Canthocamptidae

This is the largest freshwater group, widely distributed, and with more than 325 species.

1	P5 absent or of one article	2
1′	P5 composed of a baseoendopod and exopod	4
2(1)	P5 absent or lacking baseoendopod	3

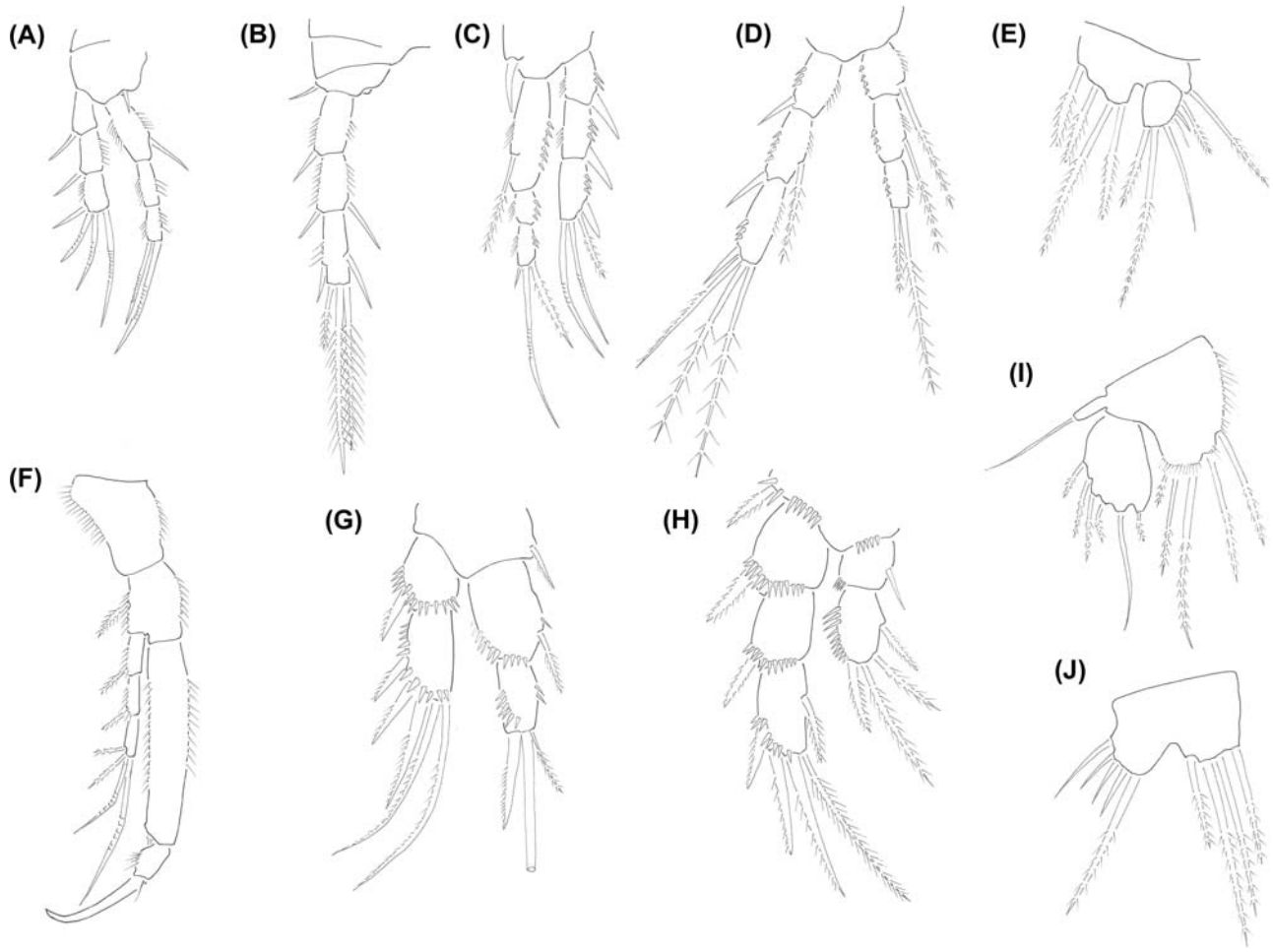


FIGURE 16.4.15 Representative structures of harpacticoid copepods: (A) *Nitocrella insularis* female P1; (B) *N. insularis* female P5; (C) *Schizopera lagrecai* female P1; (D) *S. lagrecai* female P4; (E) *S. lagrecai* female P5; (F) *Hetetolaophonte stroemii* female P1; (G) *Maraenobiotus vejdovskyi* female P1; (H) *M. vejdovskyi* female P2; (I) *H. stroemii* female P5; (J) *Ceuthonectes bulbiseta* female P5. *Not to scale. Figures redrawn from Miura, 1962 (A and B); Pesce, 1988 (C–E); Baird, 1837 (F); Mrázek, 1893 (G and H); Apostolov, 2002 (J).*

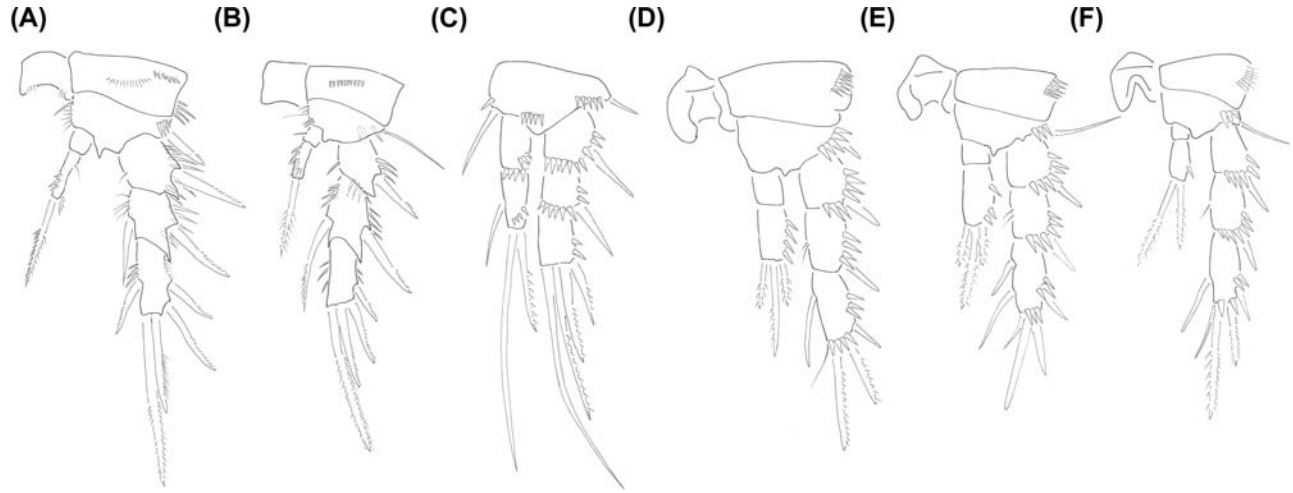


FIGURE 16.4.16 Representative structures of harpacticoid copepods: (A) *Pesceus gasparoi* female P2; (B) *P. gasparoi* female P4; (C) *Epactophanes richardi* female P1; (D) *Gulcamptus yoichiensis* female P2; (E) *G. yoichiensis* female P3; (F) *G. yoichiensis* female P4. *Not to scale. Figures redrawn from Stoch, 1998 (A and B); Ishida, 2000 (C–F).*

2′	P5 of one article (Fig. 16.4.15 J) ..... *Ceuthonectes*
3(1)	P1 endopod of two articles; antenna exopod with one seta ..... *Stygepactophanes*
3′	P1 endopod of three articles; antenna exopod with four setae ..... *Antrocamptus*
4(2)	P1 exopod of two articles 5
4′	P1 exopod of three articles 7
5(4)	Female P2 exopod of two articles 6
5′	Female P2 exopod of three articles (Figs. 16.4.15 G, H) ..... *Maraenobiotus*
6(3)	P4 second exopod lateral spine absent ..... *Hypocamptus*
6′	P4 second exopod with one lateral spine ..... *Pseudomoraria*
7(4)	P2 and P4 endopod of 1−2 articles 8
7′	P2 and P4 endopod almost reduced (Figs. 16.4.16 A, B) ..... *Pesceus*
8(7)	P2 to P4 first endopod subequal or slightly shorter than second article; rostrum large 9
8′	P2 to P4 first endopod much shorter than second article; rostrum small 10
9(8)	P4 exopod distal article with seven setae ..... *Mesochra*
9′	P4 exopod distal article with 4−5 setae ..... *Morariopsis*
10(9)	P1 second exopod without medial seta 11
10′	P1 second exopod with medial seta 18
11(10)	With a different combination of characters than below 12
11′	P2−P4 distal article as long as other two combined; P5 baseoendopod and exopod with five and four setae ..... *Pilocamptus*
12(11)	P1 endopod of three articles 13
12′	P1 endopod of two articles 14
13(12)	Cavernicolous ..... *Lessinocamptus* [Italy]
13′	Not cavernicolous ..... *Bryocamptus* (in part)
14(12)	P1 endopod reaches to or beyond midlength of exopod article three 15
14′	P1 endopod not reaching end of exopod article two (Fig. 16.4.16 C) ..... *Epactophanes*
15(14)	P2−P4 second exopod with medial seta 16
15′	P2−P4 second exopod without medial seta 17
16(15)	Cavernicolous ..... *Paramorariopsis* [Slovenia]
16′	Not cavernicolous ..... *Bryocamptus* (in part)
17(15)	P3 third exopod with one medial seta; P2 to P4 third exopod with subequal setae and spines ..... *Moraria*
17′	P3 third exopod with two medial setae; P2 to P4 third exopod medial apical seta tiny (Figs. 16.4.16 D−F) ..... *Gulcamptus*
18(10)	P1 endopod of three articles; rostrum small to moderate in size 19
18′	P1 endopod of two articles; rostrum small ..... *Bryocamptus* (in part)
19(18)	Female P5 baseoendopod penultimate lateral seta not reduced, usually equal or longer than ultimate seta; P4 endopod distal article with lateral corner bearing a distinct spine or seta 20
19′	Female P5 baseoendopod penultimate lateral seta tiny; P4 endopod distal article with lateral corner bearing a spinular process ..... *Canthocamptus*
20(19)	P1 first endopod not reaching beyond end of second exopod 21
20′	P1 first endopod reaching to or beyond third exopod midlength ..... *Attheyella* (in part)
21(20)	P2 to P4 apical exopod article with three lateral spines; female P5 baseoendopod with 5−6 setae; male P5 baseoendopod usually with two setae 22
21′	P2 to P4 apical exopod article with two lateral spines; female P5 baseoendopod with 3−4 setae; male P5 baseoendopod without setae ..... *Elaphoidella*

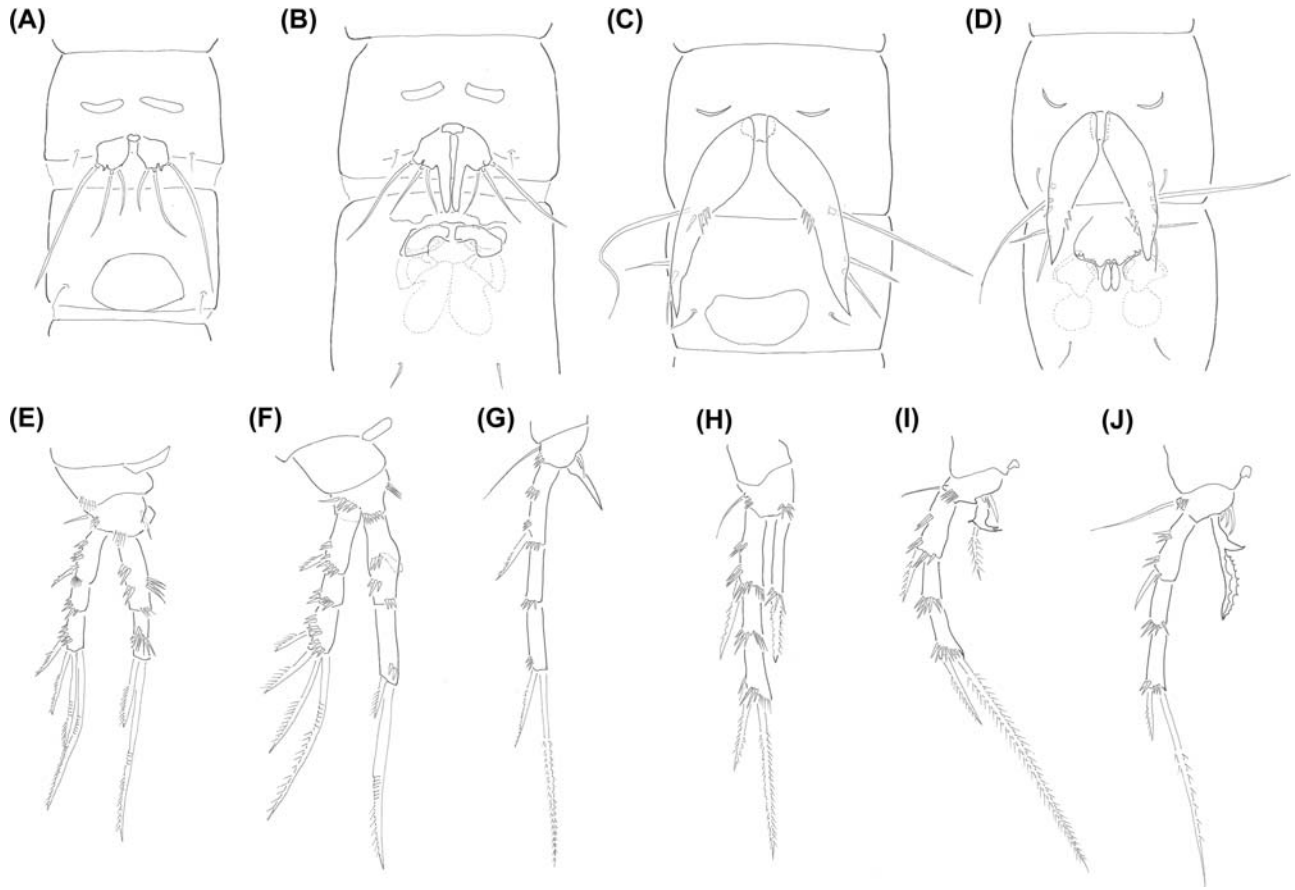


FIGURE 16.4.17 Representative structures of parastenocarid copepods: (A) Parastenocaridae nov. male P5; (B) Parastenocaridae nov. female P5 and genital field; (C) Fontonalicaridinae nov. male P5; (D) Fontonalicaridinae nov. female P5 and genital field; (E) Parastenocaridae nov. male P1; (F) Fontonalicaridinae nov. male P1; (G) *Simplicaris lethaea* male P4; (H) *Parastenocaris brevipes* male P4; (I) *Stammericaris diversitatis* male P4; (J) *Cottarellicaris etrusca* male P4. *Not to scale. Figures redrawn from Schminke, 2010 (A–F); Galassi & Laurentuus, 2004 (G); Chang, 2009 (H); Schminke, 2013 (I and J).*

22(21)	P2 and P3 endopod of 2–3 articles; female P5 baseoendopod with five setae; male P2 modified	*Bryocamptus* (in part)
22′	P2 and P3 endopod of two articles; female P5 baseoendopod with six setae; male P2 unmodified	*Attheyella* (in part)

Copepoda: Harpacticoida: Parastenocarididae: Subfamilies

Cosmopolitan, predominantly benthic. More than 250 species known, with about 108 Palaearctic species.

1	P5 mostly large; female genital field roundish and as broad as high (Figs. 16.4.17 C, D); male P1 basis without medial seta (Fig. 16.4.17 F)	Fontinalicaridinae; one genus: *Proserpinicaris*
1′	P5 mostly small or absent; female genital field rectangular (Figs. 16.4.17 A, B); male P1 basis often lacks medial seta (Fig. 16.4.17 E)	**Parastenocaridinae [p. 778]**

Copepoda: Harpacticoida: Parastenocarididae: Parastenocaridinae: Genera

1	Without the combination of characters below	2
1′	Male P4 basis medial margin with a large and slender hyaline process (Fig. 16.4.17 G)	*Horstkurtcaris*
2(1)	P5 present in both sexes	3
2′	P5 absent in both sexes	*Simplicaris*

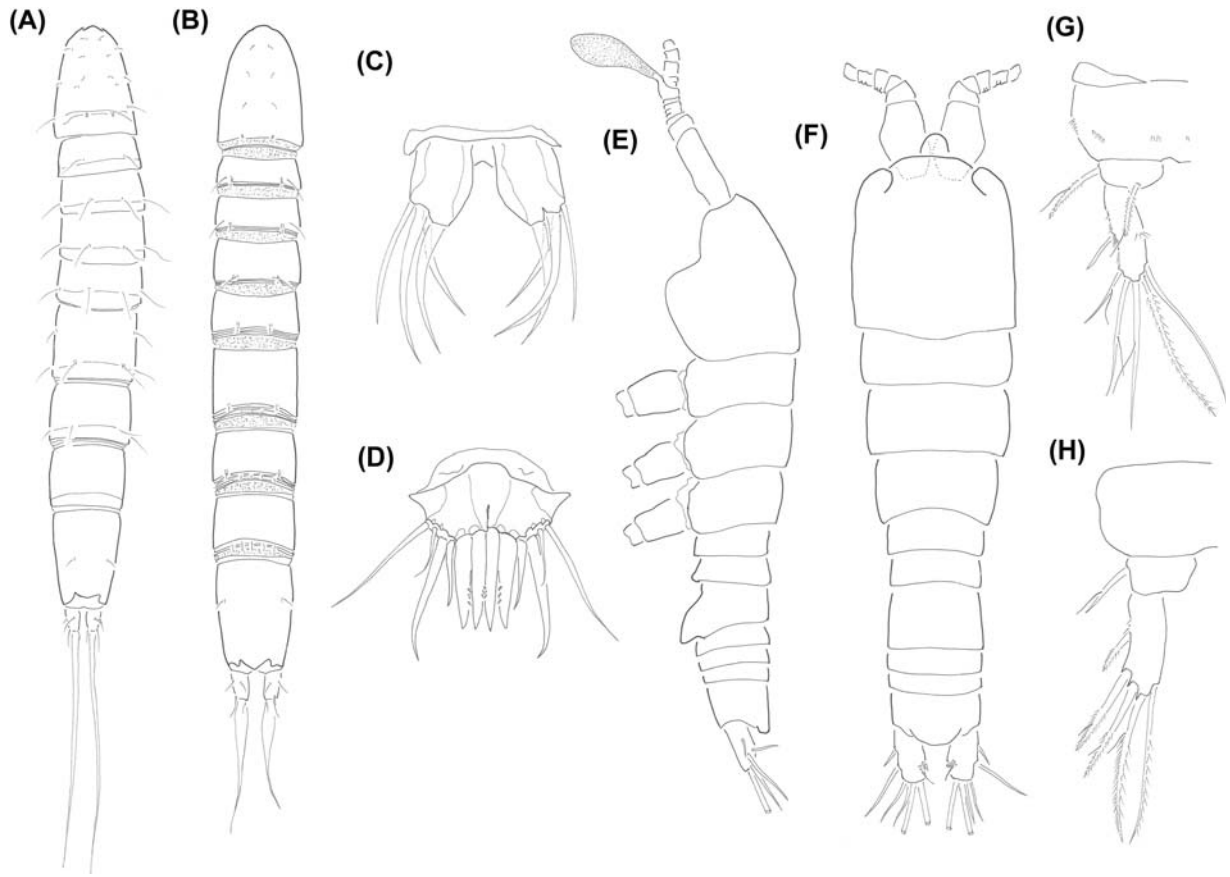


FIGURE 16.4.18 Representative structures of copepods: (A) *Leptocaris brevicornis* female habitus; (B) *Leptocaris trisetosus pacificus* female P5; (C) *L. brevicornis* male P5; (D) *L. trisetosus pacificus* male P5; (E) *Gelyella droguei* male habitus; (F) *G. drogue* female habitus; (G) *G. drogue* male P1; (H) *Gelyella monadi* male P1. *Not to scale. Figures redrawn from Chang, 2009 (A–D); Huys, 1998 (E–G); Moeschler & Rouch, 1988 (H).*

3(2)	Male P4 endopod a curved plate, with a pointed medial tip with two lateral outgrowths	4
3′	Male P4 endopod unarticulate, complex (Fig. 16.4.17 H)	*Parastenocaris*
4(3)	Male P4 endopod distal article an aciculate or plumose seat (Fig. 16.4.17 I)	*Stammericaris*
4′	Male P4 endopod distal article an elongate lamella with crenulate margins (Fig. 16.4.17 J)	*Cottarellicaris*

Copepoda: Harpacticoida: Darcythompsoniidae: *Leptocaris*: Species

Primarily marine, but with a few freshwater species.

1	Caudal rami with apical seta normal; female P5 with two setae (Figs. 16.4.18 A, C)	*Leptocaris brevicornis* van Douwe, 1905
1′	Caudal rami with apical seta broad and flat; female P5 flat with three setae (Figs. 16.4.18 B, D)	*Leptocaris trisetosus pacificus* Lee & Chang, 2008

Copepoda: Gelyelloida: Gelyellidae: *Gelyella*: Species

1	P1 and P2 distal article with six setae (Figs. 16.4.18 E–G)	*Gelyella droguei* Rouch & Lescher-Moutoué, 1977
1′	P1 and P2 distal article with five setae (Fig. 16.4.18 H)	*Gelyella monardi* Moeschler & Rouch, 1988

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Chapter 16.5

Arthropoda: Thecostraca

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Introduction to Thecostraca

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INTRODUCTION

The Thecostraca is a large and a diverse class of crustaceans with a small group of freshwater representatives that include the fish lice and barnacles. Few true freshwater barnacles occur, and most inland water taxa are brackish.

The fish lice are in great need of revision, thus no key beyond genus is provided here. At least 24 freshwater and brackish fish lice species are reported for the Palaearctic (Neethling & Avenant-Oldewage, 2016), most from Europe and Japan.



FIGURE 16.5.1 Fish louse *Argulus*: (A) ventral view of *Argulus*; and (B) external, ventral anatomy of *Argulus*. *(A) Courtesy of John Pfieffer, Ecoanalysts, Inc.*

KEYS TO CLASS THECOSTRACA

Crustacea: Thecostraca: Subclasses

1 Entirely sessile, with a calcified exoskeleton completely enclosing animal. Exoskeleton with a single, distal opening, through which the limbs are projected for filter feeding; barnacles ..... **Sessilia [p. 782]**

1′ Compound eyes present, body flattened and broad, four leg pairs, pair of large anterioventral suckers present; fish lice (ectoparasite of fish) (Fig. 16.5.1) ..... Branchiura, order Arguloida, *Argulus*

[Cosmopolitan]

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Thecostraca: Subclass Sessilia

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INTRODUCTION

Barnacles are sessile crustaceans with a permanent external calcareous shell. Charles Darwin's (1852, 1854) monographs on living Cirripedia remain a good introduction to the group. More recently, Anderson (1994) produced a good review of barnacle biology. Nearly all barnacles are exclusively marine, but a few species can tolerate reduced salinity environments in bays, estuaries, and similar habitats, as well as a few inland saline lakes.

The four barnacles that have been most successful at invading river deltas, irrigation canals, and inland water environments are in the genus *Amphibalanus* in the subfamily Amphibalaninae. Pitombo's (2004) phylogenetic analysis of the Balanidae provides the taxonomic basis for the Amphibalaninae subfamily designation. *Amphibalanus amphitrite* (Darwin, 1954), *A. eburneus* (Gould, 1841), *A. improvisus* (Darwin, 1854), and *A. subalbidus* (Henry, 1973) are species of Amphibalaninae that have been consistently successful at colonizing various harbors, river mouths, and estuaries. While *A. eburneus* is primarily restricted to harbors and river mouths, *A. improvisus* and *A. subalbidus* have successfully penetrated river and irrigation systems far inland into nearly freshwater environments. Here they often become locally abundant, perhaps as a result of ecological release from predation pressure by common marine and estuarine predators (e.g., sea stars and predatory snails) and reduced competition for living space on hard substrata.

A. amphitrite appears in saline lagoons and lakes, including most notably the Salton Sea in southern California, in addition to warm temperate and tropical harbors and estuaries. *A. improvisus* is now common in the landlocked Caspian Sea, connected to the Black and Mediterranean Seas via a system of navigable rivers and canals.

The four species of *Amphibalanus* commonly found in these environments are those most closely related to each other within the genus, based on morphological characters (Henry & McLaughlin, 1975). In their morphometric analysis of the group, Henry and McLaughlin (1975) noted that *A. amphitrite, A. subalbidus, A. eburneus*, and *A. improvisus* all have a multidenticulate labrum. Another species of barnacle, *Fistulobalanus pallidus* (Darwin, 1854), is not included in the key below because it has not yet been reported from inland waters. However, it is another euryhaline species (Sandison & Hill, 1966) that can be common in tropical harbors, estuaries, mangroves, and lagoons.

Shipping traffic has been implicated in the spread of these species from harbor to harbor as they commonly foul ship hulls and can thrive in estuarine conditions (Rocha Farrapeira et al., 2007). Human conveyance is likely the vector for introduction of the species of barnacles found in inland waters. Some of these inland populations spread more or less naturally from animals introduced to harbors. Once established in harbor areas, they often invade contiguous waters of estuaries and irrigation structures. In two cases, the Caspian Sea (12 ppt salinity, vs ∼35 ppt in seawater) and the Salton Sea in California (>44 ppt), there is evidence that inoculations of barnacles were initially introduced directly into these waters by human activity.

This work concentrates primarily on the three species (*A. amphitrite*, *A. subalbidus*, and *A. improvisus*) that have been most successful in inland waters. The related taxa that have some potential for introduction and survival in inland waters are included in the key.

TERMINOLOGY AND MORPHOLOGY

Darwin (1854, pp. 3−8) developed much of the terminology still in use today for the calcareous parts of Cirripedia. The shell wall of the Amphibalaninae species listed here consists of six plates. The four **opercular plates** that seal the opening to the shell wall are paired **terga** and **scuta**. The key below makes use of shell wall plate external coloration, shape of the terga and scuta, and major aspects of the tergal spur and basal margin. All these morphological characters should be easily discernible on cleaned specimens (see figures in species accounts herein for illustration of characters used in the key).

The small number of species compared in the key allow for the use of relatively easily seen and used characters on the shell wall and opercular plates. See the references listed herein for morphological characters and comparisons beyond the contents of the current key. Henry and McLaughlin (1975) have an especially useful explanation of terminology and characters of Amphibalaninae related to exoskeletal flexible cuticular characters, including mouthparts and setae. Darwin (1854) remains useful for calcareous part terminology. Additional terminology and more in-depth analysis of characters of opercular plates and shell wall plates, as well as flexible cuticular parts, can be found in Newman and Ross (1976) and Pitombo (2004).

MATERIAL PREPARATION AND PRESERVATION

The calcareous shell and opercular plates of barnacles are often used to make initial identifications. Although the wall plates impart some information based on color patterns and morphology, examination of the opercular plates is usually required to make an accurate identification. Fortunately, cleaning and preparing the calcareous plates for examination is relatively simple and quick. Single specimens in glass dishes or small glass containers can be treated with fresh household bleach (about 6% sodium hypochlorite) for a period of time ranging from 20 min to

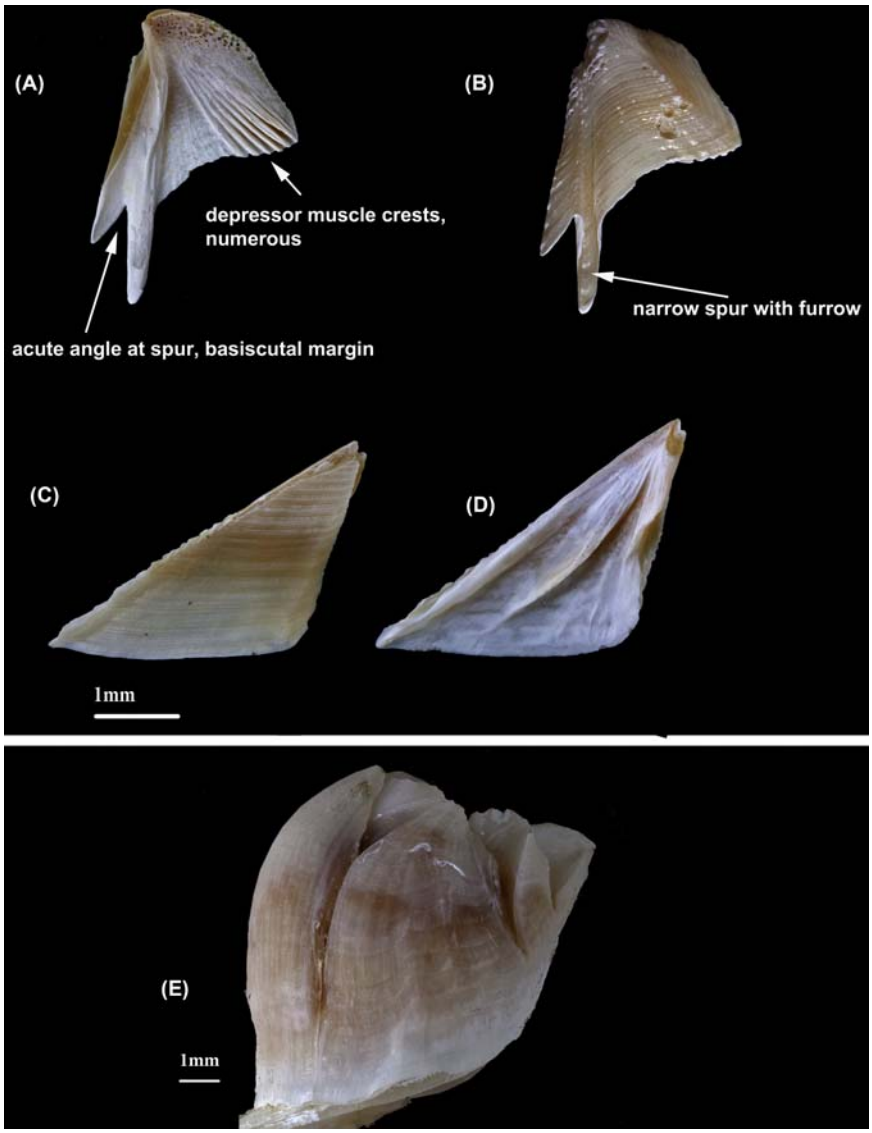


FIGURE 16.5.2 *Amphibalanus improvisus*: (A) tergum interior; (B) tergum exterior; (C) scutum exterior; (D) scutum interior; and (E) whole shell exterior side view.

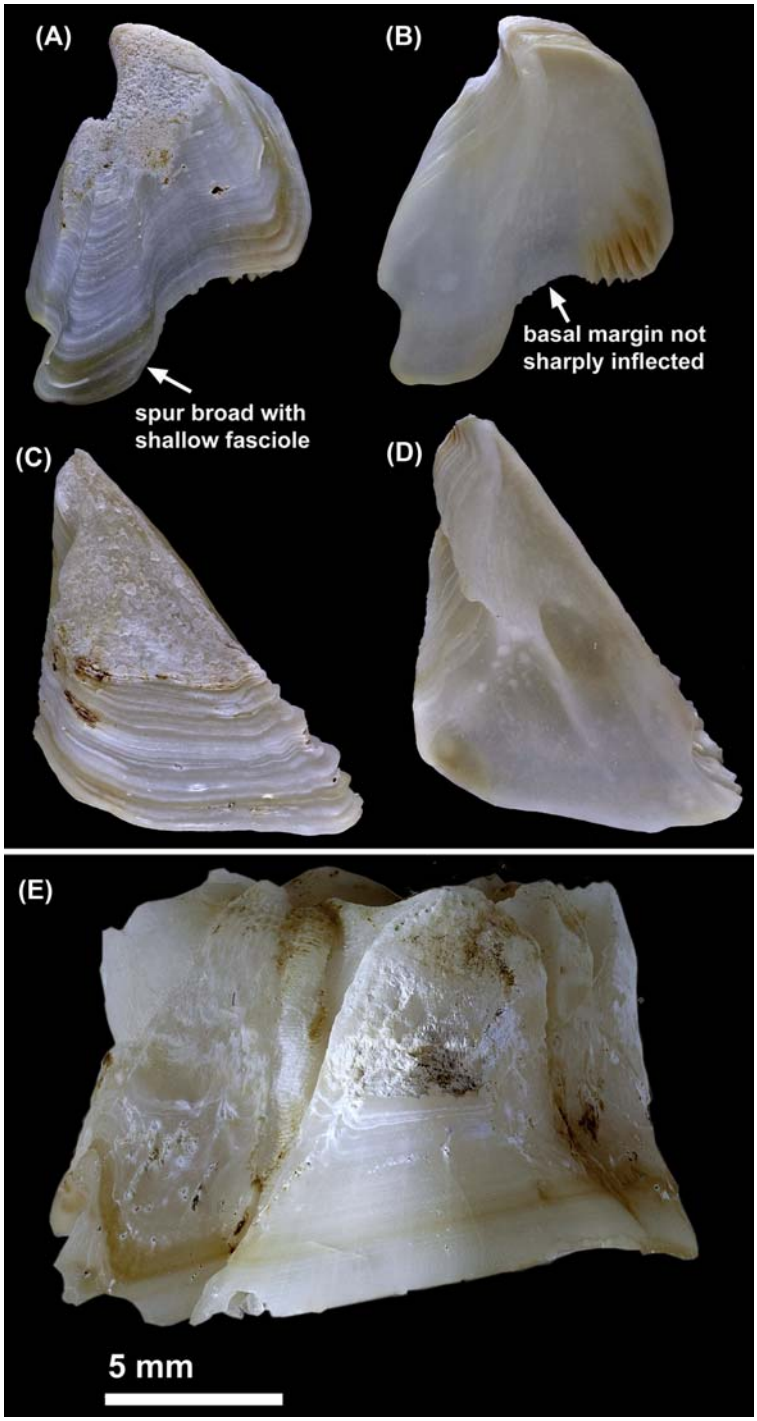


FIGURE 16.5.3 *Amphibalanus subalbidus*: (A) tergum exterior; (B) tergum interior; (C) scutum exterior; (D) scutum interior; and (E) whole shell exterior side view.

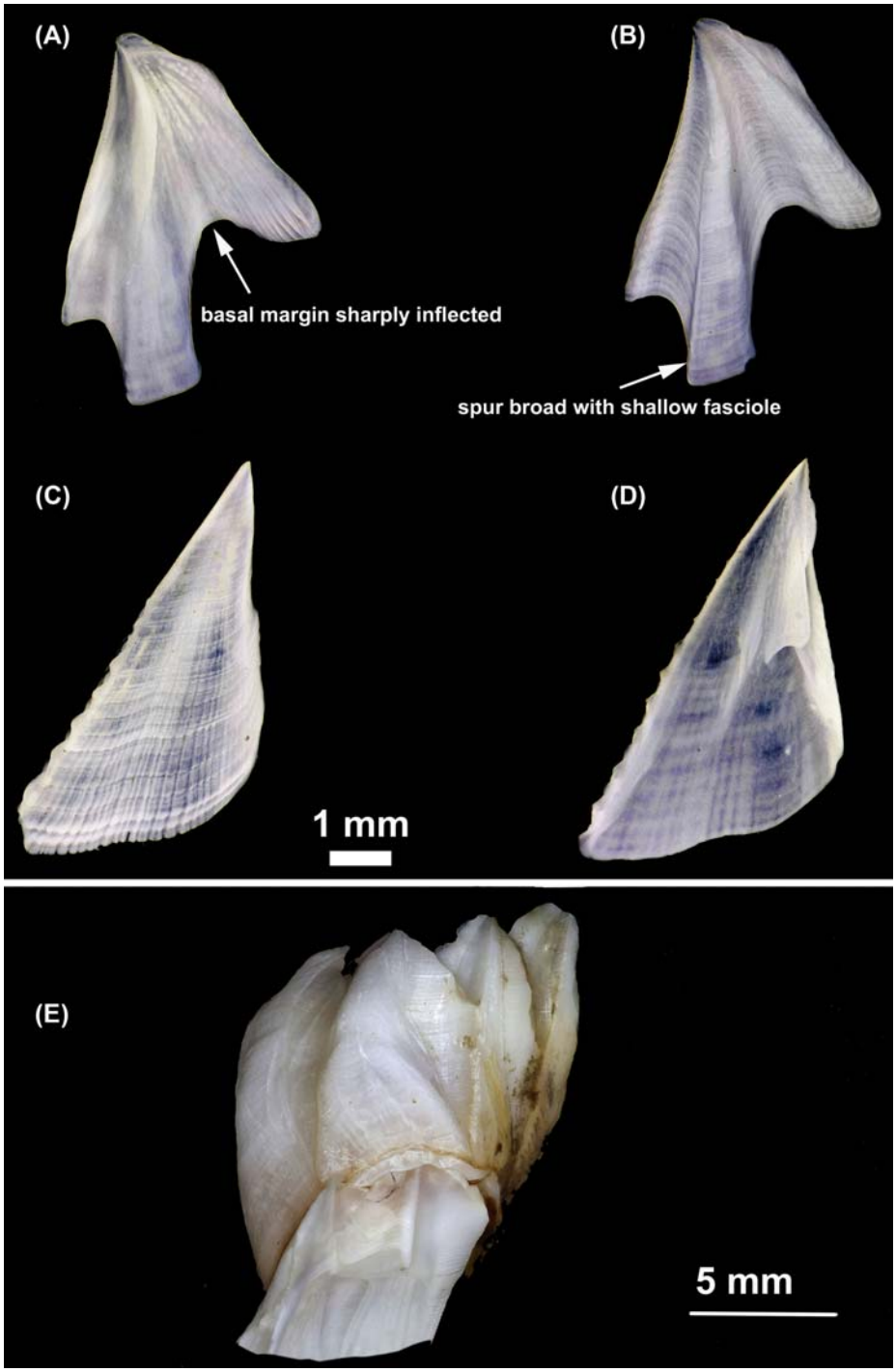


FIGURE 16.5.4 *Amphibalanus eburneus*: (A) tergum interior; (B) tergum exterior; (C) scutum exterior; (D) scutum interior; and (E) whole shell exterior side view.

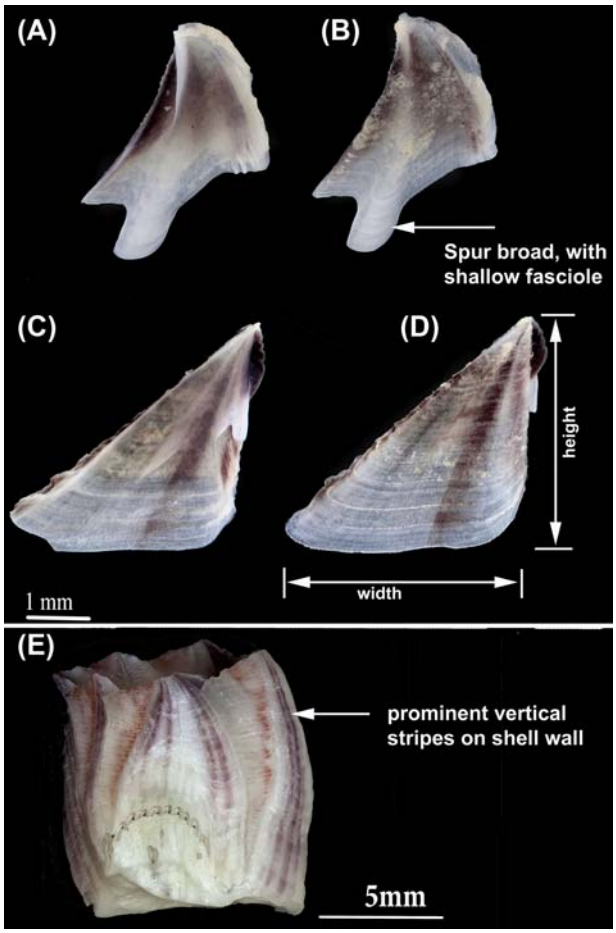


FIGURE 16.5.5 *Amphibalanus amphitrite*: (A) tergum interior; (B) tergum exterior; (C) scutum interior; (D) scutum exterior; and (E) whole shell exterior side view.

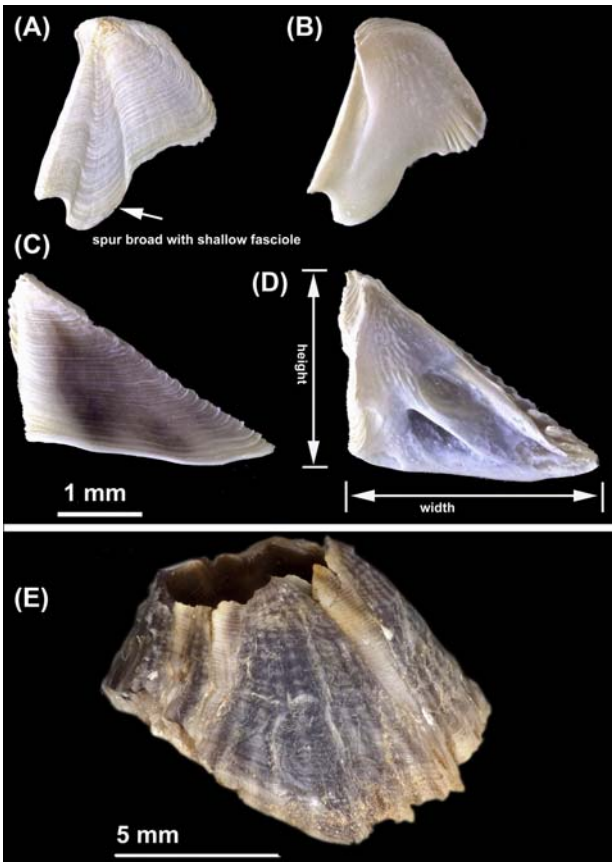


FIGURE 16.5.6 *Amphibalanus inexpectatus*: (A) tergum exterior; (B) tergum exterior; (C) scutum exterior; (D) scutum interior; and (E) whole shell exterior side view.

a few hours depending on the size of the specimens. Carefully decant the bleach from the shells after this period and gently wash them with three or more rinses in fresh water. This process will remove most, if not all, adhering tissues, thereby allowing closer examination of various shapes and structures on the plates. Carefully remove loose tissue and sediment with fine forceps or a small brush to avoid chipping and other damage to the plates. Once cleaned, the plates may be dried and stored for later examination or studied immediately using a dissecting microscope.

The exoskeletal flexible cuticular parts are also useful for identification, and some specimens should be kept intact in 75%–95% ethanol for later dissection and study of the cirri (limbs) and mouthparts. Initial and long-term preservation of tissues in 95% ethanol will also permit subsequent extraction and sequencing of DNA for molecular level studies.

KEY TO SUBCLASS SESSILIA

Thecostraca: Sessilia: *Amphibalanus*: Species

1	Exterior white, or whitish, without any vertical colored stripes	2
1′	Exterior whitish with vertical colored (purple, pink, or red) stripes (may be faded in sun-bleached dead shells)	4
2(1)	Tergum with broad spur with broad spur fasciole, sheath on wall plates often vesicular	3

2′ Tergum with narrow spur and narrow spur furrow (Fig. 16.5.2) temperate harbors, bays, estuaries, and associated irrigation canals .... *Amphibalanus improvisus* (Darwin, 1854)
[Holarctic]

3(2) Tergum basal margin flat or shallowly curved, not sharply inflected (Fig. 16.5.3); estuaries and river mouths .... *Amphibalanus subalbidus* (Henry, 1974)
[Persian Gulf. Nearctic]

3′ Tergum basal margin inflected, often sharply, on one or both sides of spur (Fig. 16.5.4); harbors and estuaries .... *Amphibalanus eburneus* (Gould, 1841)
[North Atlantic Ocean, Caspian Sea, Mediterranean Sea. Nearctic]

4(1) Scutum about same width as height (Fig. 16.5.5); tropical to warm temperate harbors and lagoons, mangroves .... *Amphibalanus amphitrite* (Darwin, 1854)
[Cosmopolitan]

4′ Scutum much wider than high (Fig. 16.5.6); tropical and subtropical bays, harbors and estuaries .... *Amphibalanus inexpectatus* (Pilsbry, 1916)
[Pacific Ocean]

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Chapter 16.6

Phylum Arthropoda: Malacostraca

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Introduction to Malacostraca

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INTRODUCTION

Malacostraca is the largest crustacean class, with about 30,000 marine, freshwater, and terrestrial species worldwide. Common features of this class are four body regions: the head (5 segments), pereon (8 segments), the pleon (6 or 7 segments), and the urosome (1−3 segments), each with jointed appendages. The head and thorax are sometimes fused into a cephalothorax, as in the Decapoda. The pereopods are variously modified for feeding, defense, and locomotion. Pleonal appendages (pleopods) may be modified for swimming, reproduction, respiration, and/or care of eggs and young.

KEYS TO MALACOSTRACA

Malacostraca: Orders

1	Carapace reduced or absent (Figs. 16.6.1−5)	2
1′	Carapace large, obvious (Figs. 16.6.6−12)	6
2(1)	Thoracopods biramous (Figs. 16.6.13−14)	3
2′	Thoracopods uniramous (Fig. 16.6.15)	4
3(2)	Body laterally compressed, abdomen diameter many times narrower than thorax (Fig. 16.6.19−21)	**Cumacea [p. 799]**
3′	Body vermiform, interstitial, less than 2 mm long (Figs. 16.6.13)	**Bathynellacea [p. 830]**
4(2)	Telson and abdominal segments fused into a pleotelson subequal in width to body (Figs. 16.6.2−5)	5
4′	Telson projecting from abdomen, telson small, narrower than body (Fig. 16.6.17)	**Amphipoda [p. 836]**
5(4)	Body dorsoventrally compressed, first pereopods chelate (Fig. 16.6.2)	**Tanaidacea [p. 855]**
5′	Body dorsoventrally compressed or subcylindrical, first pereopods as gnathopods or simple (Figs. 16.6.4 and 5)	**Isopoda [p. 857]**
6(1)	Compound eyes large pedunculate, pleopods developed and present	7



FIGURE 16.6.1 Amphipod, *Chaetogammarus ischnus* Stebbing, 1898, a Ponto-Caspian native, and invasive in Great Lakes of North America and other regions. Developing embryos are visible in the marsupium of this female. *Photograph credit: J. D. S. Witt.*



FIGURE 16.6.2 The tanaidacean *Sinlobius*. *Photograph courtesy of John Pfieffer at EcoAnalysts, Inc.*



FIGURE 16.6.3 Valviferan isopod *Chiridotea almyra*. *Photograph courtesy of Matthew A. Hill and EcoAnalysts, Inc.*



FIGURE 16.6.6 The mysid *Mysis diluviana*.



FIGURE 16.6.4 Aquatic pill bug *Gnorimosphaeroma* sp. (Sphaeromatidae). *Photograph courtesy of John Pfieffer and EcoAnalysts, Inc.*



FIGURE 16.6.7 Photograph of the dorsal view of the Chinese mitten crab *Eriocheir sinensis*. *Photograph courtesy of Matthew A. Hill and EcoAnalysts, Inc.*



FIGURE 16.6.5 The isopod *Cyathura*. *Photograph courtesy of John Pfieffer and EcoAnalysts, Inc.*

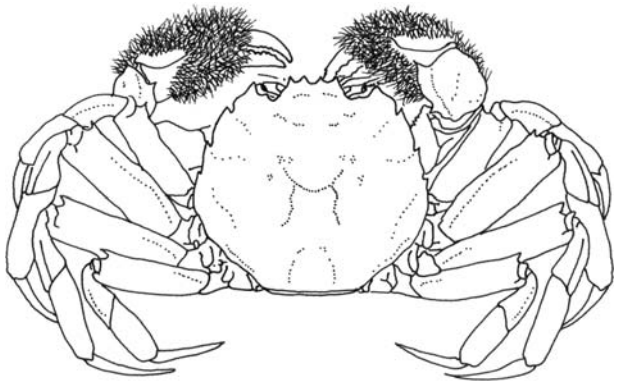


FIGURE 16.6.8 Drawing of dorsal view of the Chinese mitten crab *Eriocheir sinensis*. *From H. H. Hobbs, III in Thorp & Covich (2010).*

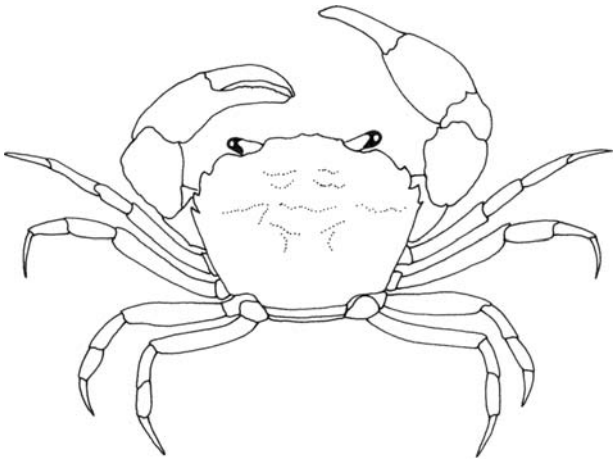


FIGURE 16.6.9 Dorsal view of the crab *Rhithropanopeus harrisii*.

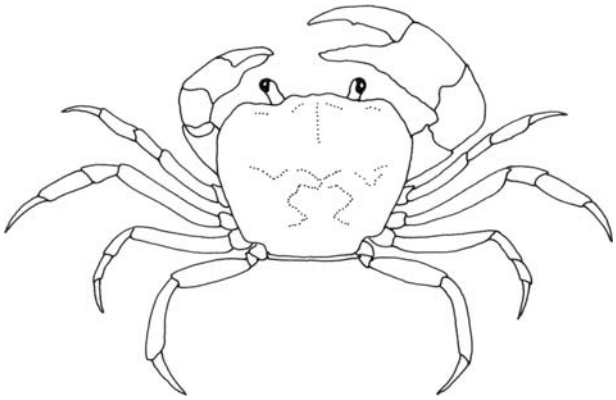


FIGURE 16.6.10 Dorsal view of *Geothelphusa dehaani*. *From H. H. Hobbs, III in Thorp & Covich (2010).*



FIGURE 16.6.11 *Cherax quadricarinatus*, the giant invasive crayfish from Australia, which has been introduced to many countries for aquaculture and the pet trade.

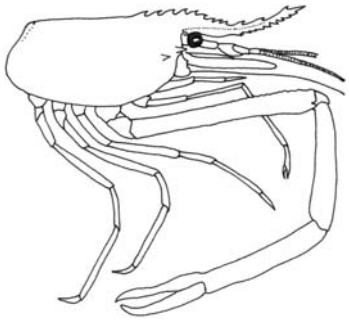


FIGURE 16.6.12 Lateral view of the carapace of *Macrobrachium rosenbergii*, a common mariculture species worldwide. *Fromm H. H. Hobbs, III in Thorp & Covich (2010).*

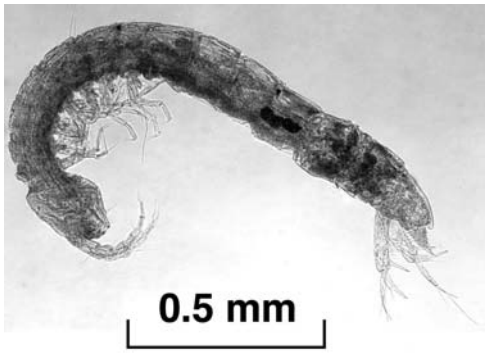


FIGURE 16.6.13 Syncarid, *Iberobathynella andalusica* Camacho 2007, female from Spain. *Photograph by A. I. Camacho.*

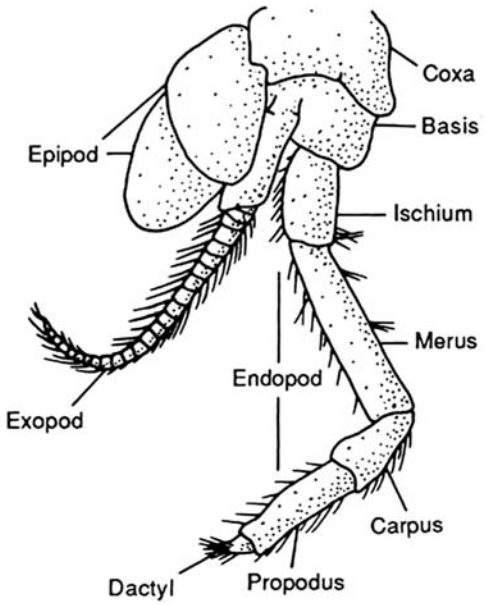


FIGURE 16.6.14 Representative crustacean appendage (from a Syncarid). *Redrawn from McLaughlin (1982).*

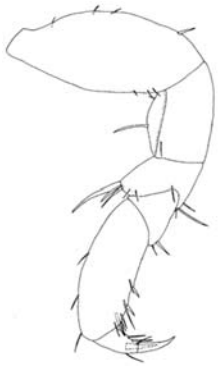


FIGURE 16.6.15 Pereopod 1 of the asellid isopod *Salmasellus howarthi*.

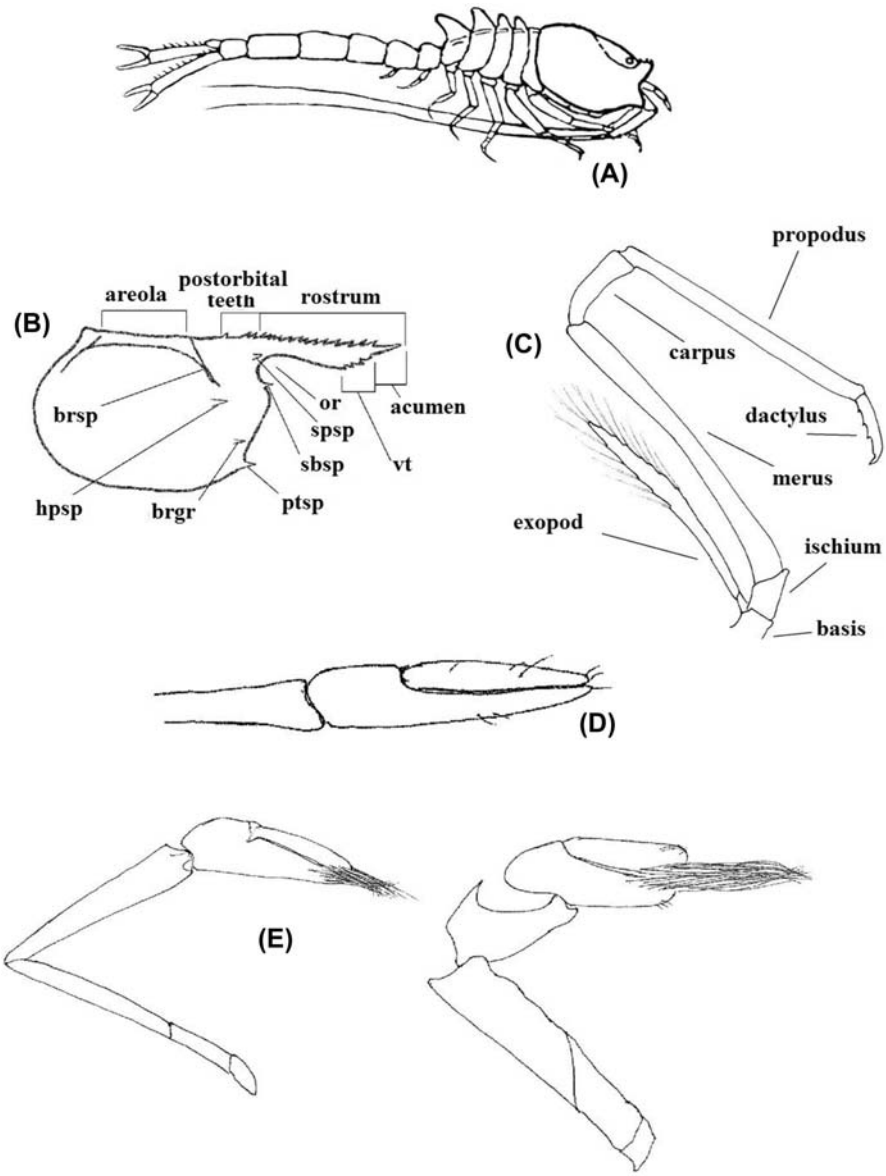


FIGURE 16.6.16 (A) *Pterocuma* sp. right lateral view; (B) generalized shrimp/crayfish carapace; (C) generalized pereopod; (D) *Macrobrachium* sp. distal portion of cheliped; (E) examples of atyid shrimp chelipeds. (*brgr*, branchyostegial groove; *brsp*, branchyostegial spine; *hpsp*, hepatic spine; *or*, orbit; *ptsp*, pterygostomial spine; *sbsp*, suborbital spine; *spsp*, supraorbital spine; *vt*, ventral teeth).



FIGURE 16.6.17 The amphipod *Eulimnogammarus parvexii* from Lake Baikal. *Photograph by Sergey Didorenko.*



FIGURE 16.6.18 The introduced and invasive crayfish *Procambarus clarki*. *Photograph courtesy of Gunter Schuster.*

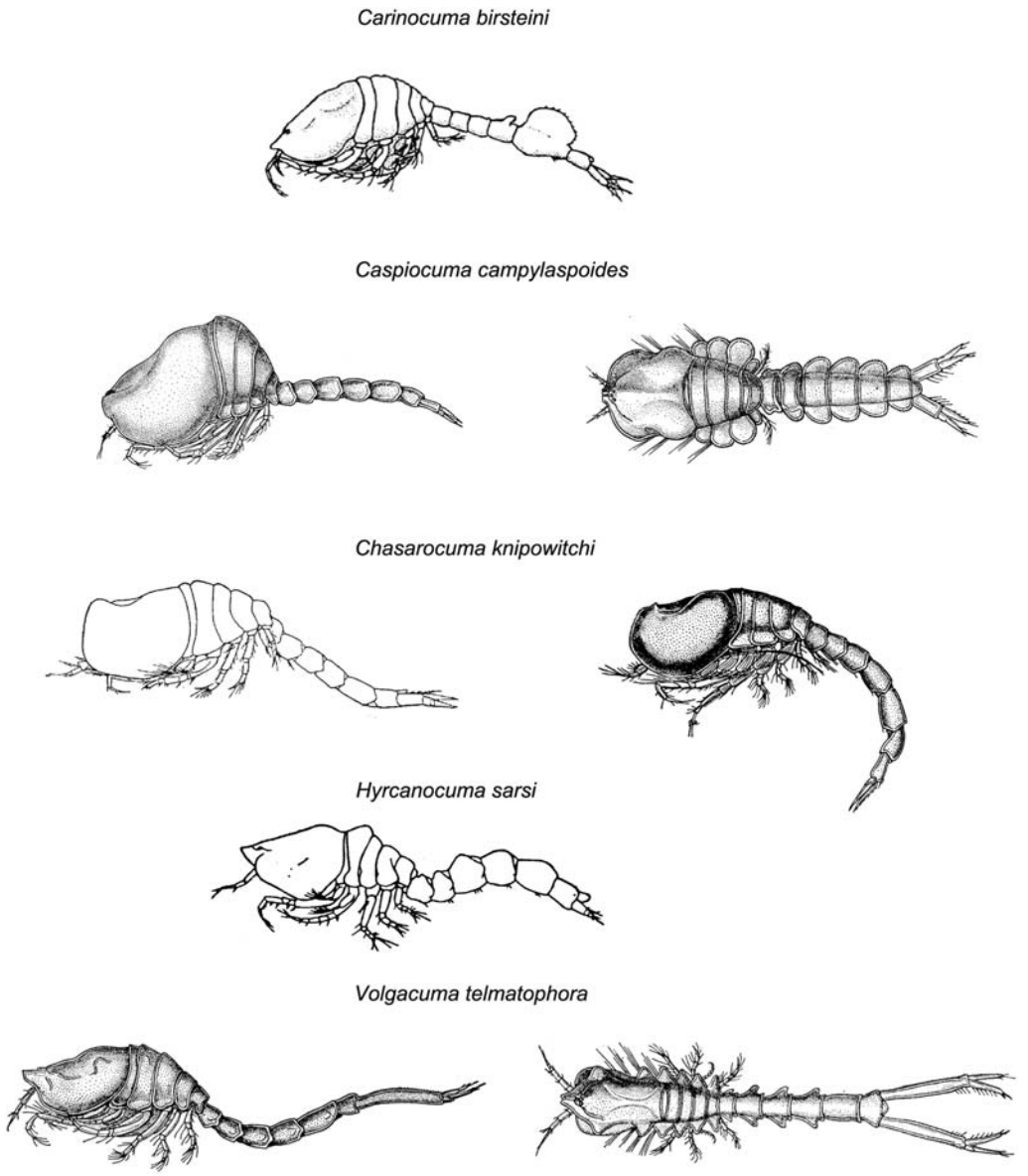


FIGURE 16.6.19 Female Cumacea individuals on left side, males on right side, when both sexes are known.

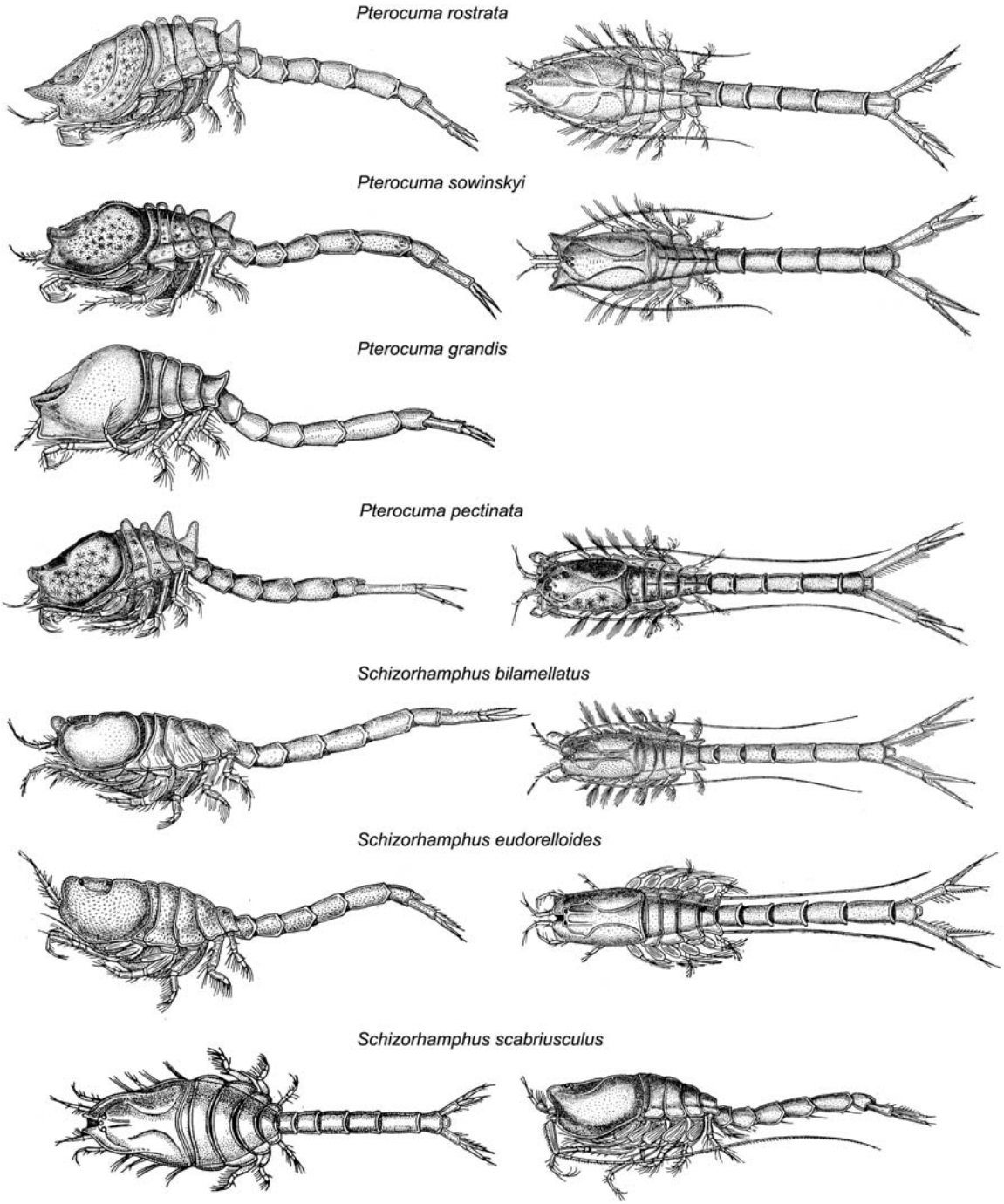


FIGURE 16.6.20 Female Cumacea individuals on left side, males on right side, when both sexes are known.

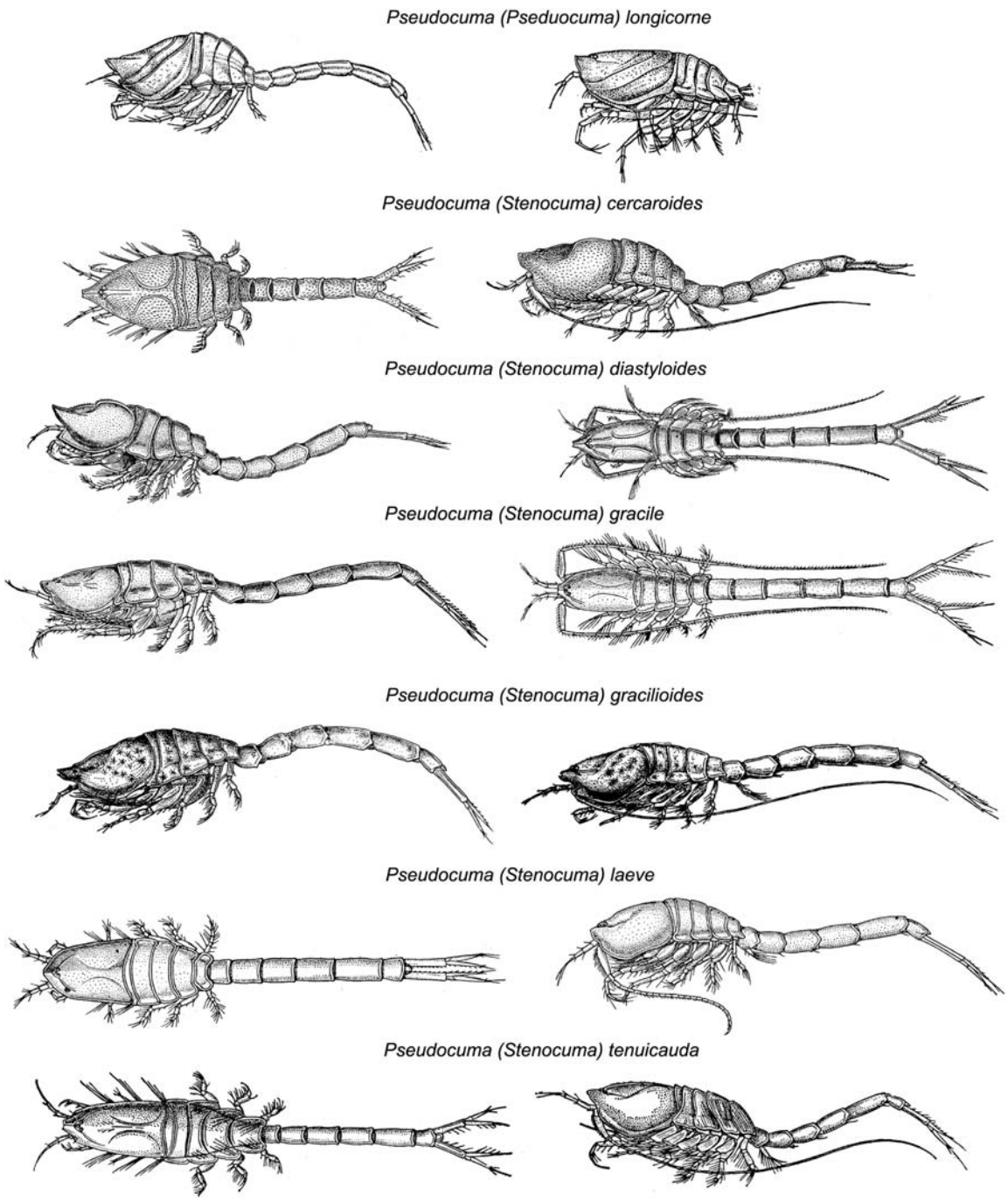


FIGURE 16.6.21 Female Cumacea individuals on left side, males on right side, when both sexes are known.

6′ Eyes absent, pleopods reduced on first abdominal segments, absent from remaining segments, eight pairs of thoracopods, first pair modified as a maxilliped ..... **Thermosbaenacea [p. 863]**

7(6) Seven pairs of thoracopods (Fig. 16.6.68) 8

7′ Five pairs of walking legs, including chelae (Figs. 16.6.7–12 and 18) ..... **Decapoda [p. 864]**

8(7) Eyes normally developed (with stalk and cornea) (Fig. 16.6.66) or without cornea (Fig. 16.6.68 A); uropodal endopod with statocyst (Fig. 16.6.67 E); uropodal protopod with no ventral medial lobe or process (Fig. 16.6.67 E) ..... Mysida, one family: **Mysidae [p. 886]**

8′ Eyes reduced to flat ocular plate with no visual elements (Figs. 16.6.67 A, B); uropodal endopod lacking statocyst (Figs. 16.6.67 C, D); uropodal protopod with a relatively short ventral medial lobe (Fig. 16.6.67 C, D) or a very long process (Fig. 16.6.2 D), bearing spiniform setae ..... **Stygiomysida [p. 883]**

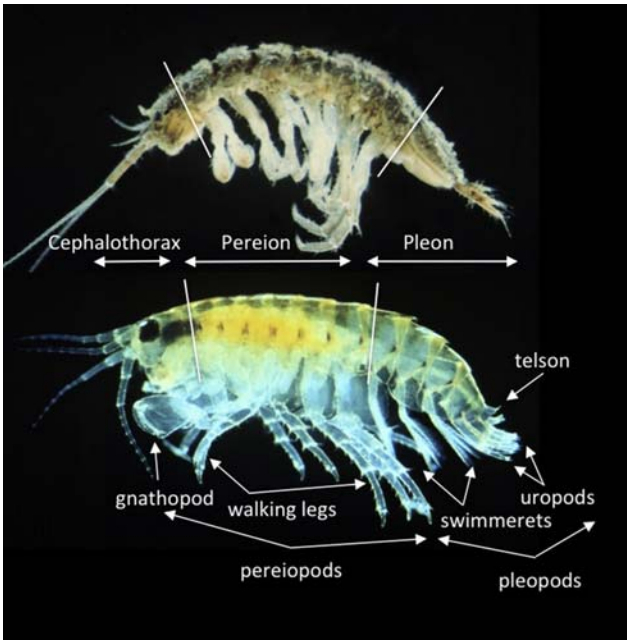


FIGURE 16.6.22 Major body regions and associated appendages in a freshwater isopod (*Caecidotea* sp.) top, and freshwater amphipod (*Hyalella* sp.), bottom. *Photographs by J. D. S. Witt.*

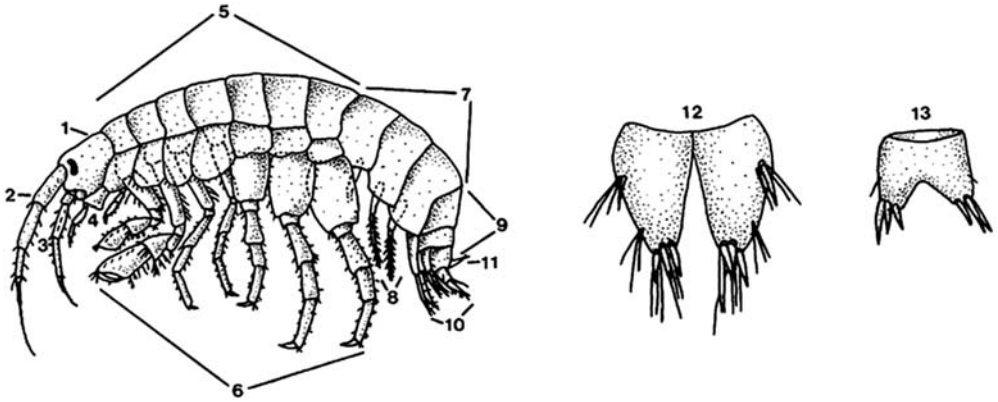


FIGURE 16.6.23 Schematic drawings of the external side view of generalized freshwater gammarid amphipods: (1) head, (2) antenna 1, (3) antenna 2, (4) mouth parts, (5) pereonites I–VII, (6) pereopods I–VII, (7) pleonites I–III, (8) pleopods I–111, (9) uronites I–III, (10) uropods I–III, (11) telson (redrawn from Holsinger (1972), (12, 13) top view of telsons for *Gammarus* and *Crangonyx*, respectively.

Malacostraca: Cumacea

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INTRODUCTION

Cumaceans are small, shrimp-like crustaceans that are very diverse in ocean waters, but have radiated slightly in brackish to fresh waters (Fig. 16.6.16). In marine waters they are found from tidal flats to the deepest parts of the abyssal basins and into at least two deep ocean trenches. They have invaded fresh or brackish water only in a few places (e.g., northeastern North America, southeastern South America) (Jaume & Boxshall, 2008). However, the radiation of cumaceans in the Ponto-Caspian region is remarkably unique. Here, there are about 20 species in eight genera, all in the Pseudocumatidae.

Cumaceans live at the sediment-water interface, usually partially buried, where they use their mouthparts to select digestible material from the uppermost few millimeters of the sediment. They can swim for short distances, usually alighting soon on a new sediment patch. Mature males, however, may swim for longer distances, and in some families have become hydrodynamically streamlined for that purpose. They may also be attracted to lights at night and can easily be caught using submerged light traps. For the most part, however, cumaceans tend to avoid the water column where they are easy prey for fish.

LIMITATIONS

The Ponto-Caspian cumaceans are described in a small number of papers (Sowinsky, 1894; Sars 1894, 1897, 1914; Derzhavin, 1912; Mordukhai-Boltovskoi & Romanova, 1973) either in English or Russian; and except for the last, are nicely summarized in Lomakina (1958). The descriptions of Sars are very detailed and should make positive identification easy, although several of his names are no longer in use. The later descriptions of Derzhavin & Mordukhai-Boltovskoi are shorter and more succinct, and the illustrations are spartan; thus those species need to be redescribed using modern standards.

Another issue that is also not fully resolved involves separation of the genera *Pseudocuma* and *Stenocuma* and variability in the morphology of *Pseudocuma longicorne*. The taxonomic decisions of Băcescu (1992) have been followed in which *Stenocuma* is nested with *Pseudocuma* as a subgenus. At present there are several subspecies that have been delineated (Băcescu, 1951) but are not distinguished here. It is not known to what extent the morphology varies in the different salinity conditions in which the species lives, or whether these subspecies represent separate evolutionary lineages.

TERMINOLOGY AND MORPHOLOGY

Cumaceans have an inflated carapace covering the first three thoracic somites, leaving a pereon of five somites. Sexes are separated in that in females pleopods are absent and the second antenna is nearly obsolescent. The thoracic appendages of the somites covered by the carapace are modified for feeding and are termed maxillipeds. A telson is always present in the Ponto-Caspian pseudocumatid cumaceans.

The cumacean carapace has one feature that distinguishes it from that of most other carapace-bearing crustaceans. The carapace anterior margin extends in front of the eyelobes to form what looks like a rostrum and so is termed a **pseudorostrum**. Between the pseudorostral extensions is the **siphon**, formed by extensions of the first maxillipeds, and which channels the exhalant respiratory current. Generally the pseudorostrum extends horizontally in front of the eyelobe, but in a few species it is bent upwards so that the siphons exit dorsally.

At the posterior end of the animal there is a pair of appendages on the last abdominal (pleon) somite. These are the uropods and they each consist of a **peduncle** and paired **rami**. The medial margin of the peduncle and medial ramus is armed with a few or many setae; these appendages are used both to help move the animal within the sediment, to help it jump from the sediment, and for grooming of the carapace.

Only features that can be readily observed using a standard stereomicroscope with little or no dissection are used in the key. In some cases forceps may need to be inserted under the carapace to pull the male antennae free. Otherwise it should not be necessary to remove any appendages.

MATERIAL PREPARATION AND PRESERVATION

Cumaceans can be readily caught by most benthic sampling gear, such as box cores or dredges. Because of their small size they are not likely to be caught by fish trawls. However, a plankton net pulled just above the substrate behind a sediment-disturbing weight of some kind will generally produce abundant specimens. Washing sediment through a

500-μm mesh sieve will easily separate specimens from other material. Specimens should be preserved in 4% formalin for 12−24 h (unless they are to be used for genetic analysis) and then stored in 70% ethanol. If put into ethanol directly, cumaceans often become brittle and limbs can break off when handled. Specimens for genetic analysis should be put directly into 95% ethanol and then the ethanol should be changed after a few hours to get rid of any remaining water that came into the specimen container with the animal.

KEYS TO CUMACEA

Cumacea: Pseudocumatidae: Genera

1	Pleonite V smooth and rounded mid-dorsally 2
1′	Pleonite V with enlarged mid-dorsal carina ..... *Carinocuma birsteini* Mordukhai-Boltovskoi & Romanova, 1973 [Caspian Sea]
2(1)	Uropods short or long, but always ≤1.5x pleonite VI length 3
2′	Uropods unusually short, peduncle and rami not much longer than pleonite VI ..... *Hyrcanocuma sarsi* Derzhavin, 1912 [Caspian Sea]
3(2)	Carapace without tubercles 4
3′	Carapace with two pairs of laterally directed tubercles; abdominal somites with lateral tubercles ..... *Volgacuma telmatophora* Derzhavin, 1912 [Caspian and Azov Seas and river deltas]
4(3)	Pereonite V without mid-dorsal carina 5
4′	Pereonite V with mid-dorsal carina; carinae also often on pereonites II−IV ..... ***Pterocuma*** **[p. 828]**
5(4)	Carapace not especially expanded or elevated posteriorly 6
5′	Carapace elevated posteriorly, much more in the female than in the male ..... *Caspiocuma campylaspoides* Sars, 1897 [Black, Azov, and Caspian seas, Volga River and other deltas]
6(5)	Pseudorostrum upturned, opens dorsally 7
6′	Pseudorostrum opens anteriorly ..... ***Pseudocuma*** **[p. 828]**
7(6)	Carapace antennal notch obsolescent or absent; male antenna II extending only to pleonite II ..... *Chasarocuma knipowitschi* Derzhavin, 1912 [Caspian, Volga R. delta]
7′	Carapace antennal notch present; male antenna II extending to end of pleon ..... ***Schizorhamphus*** **[p. 829]**

Cumacea: Pseudocumatidae: *Pterocuma*: Species

1	Pereonites II−V with a middorsal carina 2
1′	Pereonite V with a middorsal carina ..... *Pterocuma grande* (Sars, 1914) [Caspian Sea]
2(1)	Carapace smooth laterally; pseudorostral lobes not extending much beyond the eyelobe 3
2′	Carapace with lateral fold, pseudorostral lobes pointed anteriorly ..... *Pterocuma rostratum* (Sars, 1894) [Black, Azov, and Caspian Seas and river deltas]
3(2)	Pereonite IV mid-dorsal carina truncate; uropod peduncle length subequal pleonite V ..... *Pterocuma sowinskyi* (Sars, 1894) [Black, Azov, and Caspian Seas and river deltas]
3′	Pereonite IV mid-dorsal carina acute; uropod peduncle longer than pleonite V ..... *Pterocuma pectinatum* Sowinsky, 1893 [Black Sea, mouth of Danube and Dniester Rivers]

Cumacea: Pseudocumatidae: *Schizorhamphus*: Species

1	Uropod peduncles length ≥ rami; pereonite V posterior corners acute 2
1′	Uropod peduncles much shorter that rami; pereonite V posterior corners rounded ..... *Schizorhamphus scabriusculus* Sars, 1894 [Black, Azov, and Caspian Seas and river deltas]
2(1)	Carapace pseudorostral lobes extending slightly anteriorly as rounded lobes ..... *Schizorhamphus bilamellatus* Sars, 1894 [Caspian Sea]

2′ Carapace pseudorostral lobes directed dorsally, without additional lobes ..... *Schizorhamphus eudorelloides* Sars, 1894
[Black, Azov, and Caspian Seas and river deltas]

Cumacea: Pseudocumatidae: *Pseudocuma*: Species

1 Carapace without oblique lateral folds, subgenus *Stenocuma* 2

1′ Carapace with oblique lateral folds ..... *Pseudocuma (Pseudocuma) longicorne* Băcescu, 1950
[Black Sea]

2(1) Uropod peduncle length ≤4x width, rami length subequal 3

2′ Uropod peduncle length ~3x width, later ramus shorter than medial ..... *Pseudocuma cercaroides* Sars, 1894
[Black, Azov, and Caspian Seas, Volga, Danube and other river deltas]

3(2) Pseudorostral lobes acute anteriorly; male second antenna extending nearly to end of pleon 4

3′ Pseudorostral lobes blunt anteriorly; male second antenna extending only to end of pereonites ..... *Pseudocuma laeve* Sars, 1914
[Black Sea (Danube estuary), Caspian Sea]

4(3) Pseudorostral lobes short, carapace anteroventral corner weak; uropod peduncle armed with setae along entire medial margin..... 5

4′ Pseudorostral lobes long, carapace anteroventral corner pronounced; uropod peduncle medial margin without setae on proximal half to third ..... *Pseudocuma diastyloides* Sars, 1897
[Caspian Sea]

5(4) Uropod peduncle and medial ramus with medial margins bearing simple setae 6

5′ Uropod peduncle medial margin with delicately plumose setae; medial ramus with medial margin bearing simple setae .....
..... *Pseudocuma tenuicauda* Sars, 1894
[Caspian Sea, Sea of Azov]

6(5) Uropod peduncle medial margin with setae much shorter than peduncle width and widely spaced .....
..... *Pseudocuma gracilioides* Sars, 1894
[Black Sea (river deltas only), Sea of Azov, Caspian Sea]

6′ Uropod peduncle medial margin with setae subequal to peduncle width in female and exceeding peduncle width in male; setae closely spaced ..... *Pseudocuma gracile* Sars, 1894
[Caspian Sea]

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Malacostraca: Bathynellacea

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INTRODUCTION

Bathynellaceans live in the interstitial water between grains of sand and gravel. They may reach cave water or wells through cracks in the bedrock or interstitial space. Nearly nothing is known about the biology of bathynellaceans. It is assumed that they feed on detritus, bacteria, and fungi. Predatory behavior is reported for one species from Australia. Locomotion is usually a combination of swimming and crawling movement in such a way that the body is supported by the tips of the thoracopods in contact with the substrate, while limbs perform swimming movement. Some species display an escape reaction in form of free swimming.

Bathynellaceans were previously regarded as a rare taxon. However, it is now clear that they can be found almost everywhere after diligent searches. More than 270 species are currently known from all the continents except Antarctica. While most are confined to limnic groundwater, a few occur in oligo- to polyhaline waters. The fossil record extends back to the Upper Palaeozoic. Therefore, the distribution of bathynellaceans is regarded as being strongly correlated with continental drift, and a study of this group promises to yield very interesting biogeographic discoveries. However, the Bathynellacea fauna is still imperfectly known and remains to be explored over most of the world including North America, where only 17 species have thus far been reported.

LIMITATIONS

There are two families within the order Bathynellacea: Bathynellidae and Parabathynellidae. The latter family is morphologically diverse and identifying species is relative easy. More than 170 species are classified into 45 well-defined genera. In contrast, the Bathynellidae is, with a very few exception, not abundant in morphological characters, and thus its taxonomy is handicapped and unsatisfactory. Although 95 species in 27 genera have been reported, their status needs to be reexamined. This holds true especially for the many species corresponding to early discoveries and having almost no taxonomic information. Therefore, this chapter provides dichotomous keys to all genera and species of Parabathynellidae, but only to family level for Bathynellidae.

TERMINOLOGY AND MORPHOLOGY

Bathynellaceans are microscopic malacostracans (mostly 0.6–3.0 mm, sometimes up to 7.6 mm in length) having a vermiform habitus. The body consists of head, eight free thoracic segments, five free abdominal segments, and a pleotelson with furcal rami. The carapace is absent. Each thoracic segment bears a pair of thoracopods. Thoracopods I–VII are biramous, and thoracopod VIII is modified as a copulatory organ in the male or reduced in the female. The abdominal segment appendages are reduced and at most present on the first abdominal segment. The uropods are styliform and have a medial row of spines. Eyes and statocysts are absent.

MATERIAL PREPARATION AND PRESERVATION

Bathynellaceans typically inhabit the hyporheic zone of rivers or lakes, although occasionally occur in caves or in wells. The Karaman–Chappuis method (Karaman, 1935, and Chappuis, 1942) is usually used for collecting specimens, by digging a hole or driving a core to the groundwater level. The water (either through ladling or pumping) is filtered through bolting-silk plankton net (mesh size 50 um). From cave water or wells, specimens may be collected using a hand net.

Bathynellaceans are usually vulnerable to abrupt temperature changes. However, they can live for 2–3 days, when kept at a temperature similar to that of their habitat. Bathynellaceans usually have a long and tender body, which may easily deform by a high concentration fixative. They should be fixed by stages for morphological work. After fixation, specimens may be transferred into glycerol for preparation and preservation, or ethylene glycol for DNA analysis.

KEYS TO BATHYNELLACEA

Malacostraca: Bathynellacea: Families

1 Body slender, more or less throughout; pleotelson with 1−2 pairs of weaker lateral setae near the furcal rami bases; furcal rami with 3 or more than five spines along the medial and terminal margins; first antennae with 6−7 antennomeres; second antenna three, five, or six antennomeres, bent posteriorly, without exopod; labrum rim dentate or with setules; mandibular palp usually with one palpomere tipped with a long seta; first maxilla distal endite with distolateral margin bearing a group of plain setae; thoracopod I coxa without setae; thoracopods I−VII exopods with two podomeres, each with dorsal and ventral setae; female thoracopod VIII without epipod; male thoracopod VIII with exopod reduced; pleopod I usually setaform or of one podomere, or absent; uropodal sympod elongate, with the spine row arranged longitudinally; uropodal exopod often longer than endopod, sometimes with medial margin lacking setae ..... **Parabathynellidae [p. 831]**

1′ Body slender with pleon being a little more bulky than thorax; pleotelson with a pair of dorsal stout setae; furcal rami always with five terminal spines; first antenna with seven antennomeres; second antenna with 7antennomeres, directed anteriorly, with a small exopod of one podomere; labrum rim smooth; mandibular palp prehensile, with two palpomeres, and tipped with two curved, stout claws; first maxilla distal endite with distolateral margin bearing a group of plumose setae; thoracopod I coxa usually with a long plumose seta; thoracopods I−VII exopods of one podomere, with dorsal, ventral and terminal setae; female thoracopod VIII usually with epipod; male thoracopod VIII with distinct exopod; pleopod I of two podomeres; uropodal sympod rather short, with spine row oblique at its end; uropodal exopod never longer than endopod, always with medial setae ..... Bathynellidae

Malacostraca: Bathynellacea: Parabathynellidae: Genera

1 Thoracopod I exopod unarticulate, thoracopod II−VII exopod biarticulate (thoracopod VII exopod may be unarticulate) 2

1′ Thoracopod I−VII exopod at least biarticulate 7

2(1) Antenna I with six antennomeres 3

2′ Antenna I with seven antennomeres 6

3(2) Thoracopod II−IV endopod with one terminal claw 4

3′ Thoracopod II−VII endopod with two terminal claws 5

4(3) Thoracopod II−IV endopod with one terminal claw ..... ***Hexabathynella* [p. 832]**

4′ Thoracopod II−IV endopod with one terminal claw and one seta ..... ***Arisubathynella* [p. 832]**

5(3) Thoracopod II−VII endopod with two terminal claws ..... ***Nipponbathynella*** (in part)

5′ Thoracopod II−VII endopod with two terminal claws and one seta ..... ***Iberobathynella* [p. 833]**

6(2) With six thoracopod pairs ..... ***Hexaiberobathynella* [p. 835]**

6′ With seven thoracopod pairs ..... ***Iberobathynella*** (in part)

7(1) Thoracopods I−VII with exopod of two articles 8

7′ At least some thoracopods with the exopod of more articles 14

8(7) Antenna I with seven antennomeres 11

8′ Antenna I with <seven antennomeres 9

9(8) Antenna I terminal antennomere with four terminal setae 10

9′ Antenna I terminal antennomere with fewer than four terminal setae ..... ***Nipponbathynella*** (in part)

10(9) Furca with three spines ..... ***Eobathynella* [p. 835]**

10′ Furca with more spines ..... ***Allobathynella*** (in part)

11(9) Antenna II of three or four antennomeres 12

11′ Antenna II with >four antennomeres 13

12(11) Labrum main teeth hamulate; maxilla I distal endite with hamulate claws ..... *Guadalopebathynella puchi* Camacho & Serban, 1998 [Spain]

12′ Labrum main teeth serrate; maxilla I distal endite with normal claws ..... ***Iberobathynella*** (in part)

13(11) Antenna II with five antennomeres, penultimate one with setae; thoracopod I without epipod; thoracopods II−VII endopod first article without long lateral seta ..... *Parabathynella*

13′ Antenna II with six antennomeres, penultimate one without setae; thoracopod I−III without epipod; thoracopods II−VII endopod first article with long lateral seta ..... *Issykkulibathynella tianschanica* Jankowskaja, 1964 [Russia]

14(7)	Antenna I with <10 articles	15
14′	Antenna I with 10 articles	*Sinobathynella decamera* Camacho, Trontelj & Zagmajster, 2006 [China]
15(14)	Antenna I with <eight articles	16
15′	Antenna I with eight articles	***Allobathynella*** (in part)
16(15)	Antenna I with seven articles	17
16′	Antenna I with six articles	***Iberobathynella*** (in part)
17(16)	Antenna II with more than three articles	18
17′	Antenna II with three articles	***Iberobathynella*** (in part)/***Paraiberobathynella***
18(17)	First abdominal somite without pleopods	19
18′	First abdominal somite with pleopods	***Allobathynella*** (in part)
19(18)	Antenna II terminal article with four setae, penultimate article with setae	***Allobathynella*** (in part) (*kuma*)
19′	Antenna II terminal article with three setae, penultimate article without setae	***Eobathynella*** **[p. 835]**

Malacostraca: Bathynellacea: Parabathynellidae: *Hexabathynella*: Species

1	First abdominal somite without remnants of pleopods	2
1′	First abdominal somite ventrally with two setae as remnants of pleopods	3
2(1)	Uropod endopod with three setae	*Hexabathynella valdecasasi,* Camacho, 2004 [Spain]
2′	Uropod endopod with two setae	*Hexabathynella nicoleiana* Camacho, 1986 [Spain]
3(2)	Uropod Exopod not falcate and with more than one seta	4
3′	Uropod Exopod falcate and with one set; taxonomy unclear *Hexabathynella hebrica* Cvetkov & Petrova, 1964, *Hexabathynella nestica* Cvetkov, 1970, *Hexabathynella breviappendiculata* Cvetkov, 1970, *Hexabathynella longiappendiculata* Cvetkov, 1970,	*Hexabathynella tenera* Cvetkov, 1968 [Bulgaria]
4(3)	Uropod sympod with row of inhomonomous spines	5
4′	Uropod sympod with row of homonomous spines	*Hexabathynella sevillaensis* Camacho, 2005 [Spain]
5(4)	Uropod sympod with one setaform spine and a thicker and longer distal spine; furcal rami dorsolateral setae subequal	*Hexabathynella knoepffleri* Coineau, 1964 [France]
5′	Uropod sympod with two tiny spines and a thicker and much longer distal spine; furcal rami dorsolateral lateral seta length 6x medial seta	*Hexabathynella minuta* Noodt & Galhano, 1969 [Portugal, Spain]

Malacostraca: Bathynellacea: Parabathynellidae: *Arisubathynella*: Species

1	First antenna, antennomere I with one medial seta	2
1′	First antenna, antennomere I with two medial setae	*Arisubathynella imjinensis* Park & Cho, 2015 [Korea]
2(1)	Thoracopod I endopod article IV with two claws and one seta	*Arisubathynella cheongmiensis* Park & Eun, 2012 [Korea]
2′	Thoracopod I endopod article IV with two claws	*Arisubathynella hongcheonensis* Park & Cho, 2015 [Korea]

Malacostraca: Bathynellacea: Parabathynellidae: *Nipponbathynella*: Species

Nipponbathynella miurai (Uéno, 1952) is excluded due to the incomplete description.

1	Thoracopods with basipod lateral margin smooth	2

1′	Thoracopods with basipod lateral margin bearing robust setae	*Nipponbathynella shigaensis* Park & Cho, 2015 [Japan]
2(1)	Second antennae with lateral setae simple	3
2′	Second antennae with lateral setae plumose	*Nipponbathynella uozumii* Morimoto, 2002 [Japan]
3(2)	First antenna, antennomere I with plumose setae dorsolaterally and laterally	4
3′	First antenna, antennomere I with plumose setae dorsolaterally, laterally and ventrolaterally	5
4(3)	Uropod baciliform	*Nipponbathynella wanjuensis* Park & Cho, 2015 [Korea]
4′	Uropod pectinate	*Nipponbathynella pectina* Cho, Hwang & Nam, 2008 [Korea]
5(3)	Male thoracopod VIII exopod with three spinules and two teeth	*Nipponbathynella leesookyungae* Park & Cho, 2015 [Korea]
5′	Male thoracopod VIII exopod smooth	*Nipponbathynella donggangensis* Park & Cho, 2015 [Korea]

Bathynellacea: Parabathynellidae: *Iberobathynella* and *Paraiberobathynella*: Species

Both genera need to be revised.

1	First antenna of six articles	2
1′	First antenna of articles	3
2(1)	Uropod endopod with two setae; uropod exopod with basiventral seta; uropod sympod with row of nine spines; anal operculum not pronounced	*Iberobathynella guarenensis* Camacho, 2003 [Spain]
2′	Uropod endopod with three setae; uropod exopod without basiventral seta; uropod sympod with row of five spines; anal operculum pronounced	*Iberobathynella celiana* Camacho, 2003 [Spain]
3(1)	Uropod endopod without setae	4
3′	Uropod endopod with setae	5
4(3)	Uropod sympod with homonomous row of 12 spines; uropod exopod without basiventral seta; furcal rami with eight spines; thoracopod I exopod of two articles	*Iberobathynella burgalensis* Camacho, 2005 [Spain]
4′	Uropod sympod with inhomonomous row of six spines; uropod exopod with basiventral seta; furcal rami with five spines; Thoracopod I exopod one article	*Iberobathynella cornejoensis* Camacho, 2005 [Spain]
5(3)	Uropod endopod with one seta	6
5′	Uropod endopod with more setae	13
6(5)	Thoracopod I exopod of more than one article	7
6′	Thoracopod I exopod one article	11
7(6)	Thoracopod I exopod of two articles	8
7′	Thoracopod I exopod of three articles	*Paraiberobathynella notenboomi* Camacho, 1989 [Spain]
8(7)	Thoracopod II–VII exopod of two articles	9
8′	Thoracopod II–VII exopod of three articles	10
9(8)	Uropod exopod with four setae; mandible spine row with 5–6 claws	*Iberobathynella espaniensis* Serban & Comas I Navarro, 1978 [Spain]
9′	Uropod exopod with five setae; mandible spine row with eight claws	*Iberobathynella magna* Camacho & Serban, 1998 [Spain]
10(8)	Uropod with endopod and exopod subequal	*Paraiberobathynella maghrebensis* Boutin & Coineau, 1987 [Algeria, Morocco]

10′	Uropod with endopod longer than exopod ..... *Paraiberobathynella fagei* Delamare Deboutteville & Angelier, 1950 [Spain]
11(6)	Uropod exopod with four terminal setae 12
11′	Uropod exopod with only two terminal setae ..... *Iberobathynella serbani* Camacho, 2003 [Portugal]
12(11)	Maxilla I distal endite with six claws ..... *Iberobathynella imuniensis* Camacho, 1987 [Spain]
12′	Maxilla I distal endite with seven claws ..... *Iberobathynella cantabriensis* Camacho & Serban, 1998 [Spain]
13(5)	Thoracopod I exopod of one article; thoracopods II−VII endopod first article without lateral seta 14
13′	Thoracopod I exopod of two articles; copods II−VII endopod first article with lateral seta 20
14(13)	Uropod endopod with three setae (one is minute in *I. rouchi*); maxilla II first article with one seta 15
14′	Uropod endopod with two setae; maxilla II first article without setae 16
15(14)	Uropod exopod with four setae; anal operculum with medial protrusion; thoracopod I endopod article II with two medial setae ..... *Iberobathynella andalusica* Camacho, 2007 [Spain]
15′	Uropod exopod with three setae; anal operculum without medial protrusion; thoracopod I endopod article II with one medial seta ..... *Iberobathynella rouchi* Camacho & Coineau, 1987 [Spain]
16(14)	Uropod exopod with three setae 17
16′	Uropod exopod with two terminal setae ..... *Iberobathynella cavadoensis* Noodt & Galhano, 1969 [Spain, Portugal]
17(16)	Thoracopod I endopod article I with one medial seta; maxilla II distal endite with six claws 18
17′	Thoracopod I endopod article I with two medial setae; maxilla II distal endite with seven claws ..... *Iberobathynella pedroi* Camacho, 2003 [Portugal]
18(17)	Uropod endopod setae not reaching endopod apex; furca dorsolateral seta length ≤ furcal ramus 19
18′	Uropod endopod setae reaching just beyond endopod apex; furca dorsolateral seta length > furcal ramus ..... *Iberobathynella lamasonensis* Camacho, 2005 [Spain]
19(18)	Furcal rami with 8−9 spines; female thoracopod VIII cuticle wrinkled; first antenna, antennomere V with one aesthetasc ..... *Iberobathynella asturiensis* Serban & Comas I Navarro, 1978 [Spain]
19′	Furcal rami with seven spines; female thoracopod VIII cuticle smooth; first antenna, antennomere V with two aesthetascs ..... *Iberobathynella ortizi* Camacho, 1989 [Spain]
20(13)	Thoracopod I exopod of two articles with four setae 21
20′	Thoracopod I exopod of two articles with five setae 22
21(20)	Uropod exopod with four setae ..... *Iberobathynella lusitanica* Braga, 1949 [Portugal]
21′	Uropod exopod with seven setae ..... *Iberobathynella barcelensis* Noodt & Galhano, 1969 [Portugal]
22(21)	Uropod sympod with row of 16−22 spines; thoracopods II−VI or II−V exopods with five setae 23
22′	Uropod sympod with row of 9−11 spines; thoracopods II−VI exopods with five setae ..... *Iberobathynella valbonensis* Galhano, 1970 [Spain, Portugal]
23(22)	Uropod sympod with row of 16−19 spines; furcal rami with 8−9 spines; thoracopods II−VI exopods with five setae ..... *Iberobathynella gracilipes* Braga, 1960 [Portugal]
23′	Uropod sympod with row of 17−22 spines; furcal rami with 9−11 spines; thoracopods II−V exopods with five setae ..... *Iberobathynella paragracilipes* Camacho & Serban, 1998 [Spain]

Malacostraca: Bathynellacea: Parabathynellidae: *Hexaiberobathynella*: Species

1 Uropod sympod length 3x width, bearing a spine row with 6–8 spines, distal spine reaching two-thirds of endopod length; furcal rami with 5–7 spines; anal operculum protruding ..... *Hexaiberobathynella mateusi* Galhano, 1967 [Spain, Portugal]

1′ Uropod sympod length 6x width, spine row with 10–15 spines, distal spine reaching one-third of endopod length; furcal rami with 10–15 spines; anal operculum not protruding ..... *Hexaiberobathynella hortezuelensis* Camacho & Serban, 1998 [Spain]

Malacostraca: Bathynellacea: Parabathynellidae: *Eobathynella*: Species

1 First antenna with six antennomeres; thoracopods II–VII exopods of two articles; thoracopod II–VII endopod proximal article without lateral seta; furcal rami with few spines; uropod sympod with row of few spines 2

1′ First antenna with seven antennomeres; thoracopods II–VII exopods of more than two articles; thoracopods II–VII endopods proximal article with lateral seta; furcal rami with five spines; uropod sympod with row of 11 spines ..... *Eobathynella mesasiatica* Birstein & Ljovuschkin, 1964 [Russia]

2(1) Thoracopods I–II without epipod; furcal rami with three spines; uropod sympod with row of 6–8 spines 3

2′ Thoracopods I–III without epipod; furcal rami with four spines; uropod sympod with row of five spines ..... *Eobathynella minima* Jankowskaja, 1972 [Uzbekistan]

3(2) Uropod endopod with medial spine(s); uropod exopod with lateral seta; thoracopod I exopod of two articles 4

3′ Uropod endopod without medial spine; uropod exopod without lateral seta; thoracopod I exopod of one article ..... *Eobathynella matuta* Morimoto, 1970 [Korea]

4(3) Uropod endopod without proximal dorsal plumose seta; mandible *pars incisiva* with three teeth ..... *Eobathynella gracillima* Uéno, 1956 [Japan]

4′ Uropod endopod with proximal dorsal plumose seta; mandible *pars incisiva* with four teeth ..... *Eobathynella yeojuensis* Schminke, 2010 [Korea]

Malacostraca: Bathynellacea: Parabathynellidae: *Allobathynella*: Species

1 First antenna of eight articles; uropod sympod with spine row with 2–3 distalmost spines longer; female thoracopod VIII with 2–4 terminal setae 2

1′ First antenna of fewer than eight articles; uropod sympod with subequal spine row; female thoracopod VIII with ≤1 terminal seta 3

2(1) Thoracopods I–IV without epipod; female thoracopod VIII with four terminal setae ..... *Allobathynella gigantea gigantea* Morimoto, 1959 [Japan]

2′ Thoracopods I–III without epipod; female thoracopod VIII with two terminal setae ..... *Allobathynella gigantea pluto* Morimoto, 1963 [Japan]

3(1) Uropod endopod without additional medial margin spines; pleopods absent 4

3′ Uropod endopod with additional medial margin spines; pleopods present 6

4(3) First antenna of seven articles; thorcaopods I and II with epipod rudimentary or absent; posterior somites weakly or not carinate; uropod exopod with two terminal setae plus a basiventral seta 5

4′ First antenna of six articles; thoracopods I–VII with epipod; somites dorsally carinate; uropod exopod with three setae, without basiventral seta ..... *Allobathynella carinata* Uéno, 1952 [Japan]

5(4) Furcal rami with three spines; uropod sympod with row of 6–7 spines; uropod endopod with one large terminal spine ..... *Allobathynella yaye* Uéno, 1956 [Japan]

5′ Furcal rami with five spines; uropod sympod with row of 14 or 15 spines; uropod endopod with two large terminal spines ..... *Allobathynella kuma* Uéno, 1956 [Japan]

6(3) Thoracopods I and II without epipod; thoracopod VII exopod of four articles 7

6′ Thoracopods I–III without epipod; thoracopod VII exopod of five articles 8

7(6) Uropod sympod with row of 5–6 spines; mandible palp with one seta ..... *Allobathynella japonica* Morimoto & Miura, 1957 [Japan]

7′ Uropod sympod with row of 10 spines; mandible palp with two setae ..... *Allobathynella coreana* Morimoto, 1970 [Korea]

8(6) Uropod sympod with fewer spines; uropod endopod with five spines; thoracopod VII with epipod; mandible palp with two setae 9

8′ Uropod sympod with row of 12 spines; uropod endopod with six spines; thoracopod VII without epipod; mandible palp with one seta ..... *Allobathynella mirabilis* Uéno, 1961 [Japan]

9(8) Uropod sympod with row of 10 spines; furcal rami with six spines ..... *Allobathynella shinjongieei* Park & Cho, 2008 [Korea]

9′ Uropod sympod with row of eight spines; furcal rami with five spines ..... *Allobathynella coreana* Morimoto, 1970 [Korea]

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Malacostraca: Amphipoda

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INTRODUCTION

Amphipoda are present in all types of continental waters; springs, rivers, lakes, and are richly represented in subterranean interstitial and cave systems. They are less numerous in Palearctic terrestrial habitats. Approximately 1500 non-marine species have been described from Palearctic waters, of which several hundred (more than 350) are endemic to Lake Baikal. These numbers are still growing.

LIMITATIONS

In amphipods, homoplasies are such a common occurrence that molecular and morphological phylogenies completely disagree. Therefore, these keys only partially follow phylogenetic relationships and focus on the most obvious, easily visible, and easily accessible characters. Uropod III is the structure most often used. Morphologically aberrant members of accepted genera are common; therefore some names may occur several times throughout the keys. In most cases, males are easier to identify than the more variable juveniles and females. Identification is very often uncertain. If your identification is questionable (e.g., not in agreement with geographical definition), check additional individuals (but remember that different species and genera may occur together in the same locality), try alternative pathways or keys, or check against the descriptions in the literature.

We took the nominal genera for granted, uncritically, but note that many will be reduced to synonymy after molecular phylogenetic analyses. Particularly unreliable taxa are those grounded on reductions or lack of characters.

The same may eventually be true for some families. In most large genera, some characters are highly variable; such is the case of pereopod article shapes and widths, the form of maxilla I apical spines, et cetera.

TERMINOLOGY AND MORPHOLOGY

The basic morphological terms are presented in Figs. 16.6.22 and 26 from Volumes I and II, respectively. The head bears a pair of **eyes** that are usually pigmented; if such pigmentation is missing, we usually say that the eyes are absent, although their structures are still developed under the integument. The head bears two pairs of antennae. The upper pair is **antenna I**, with a basal **peduncle** of three articles and a **distal flagellum** of many articles. An accessory flagellum may be attached at the mediodistal end of peduncle article 3, and it is usually composed of one to several tiny, elongate, cylindrical (**bacilliform**) **articles**. It may be difficult to observe if it is very small, uniarticulate, rudimentary, or scaliform.

The mandibles, maxillae I and II, and maxillipeds are in a complex on the head ventral surface. Pereopods I and II are modified as **gnathopods**, designed for grasping, usually with articles 6 and 7 as subchelae, rarely as chelae. Pereopods I–IV have the coxae transformed into large coxal plates, while coxae V–VII are smaller than the enlarged and flattened article 2 of those pereopods. Thus, when counting pereopod articles do not neglect the **coxa**; if in doubt, start with the distal **dactylus**, which is article 7, and count backwards. As an article length may need to be determined, measure from one articulation point to the next, not using the longest article axis. The last three limbs are the **uropods**. Uropod III is close to the anus. Above the anus is attached the tiny telson, the final body segment.

Uropod III usually appears as a pair of double or quadruple tails at the posterior end of the body. If they are not visible, they may be either very small (may be shorter than telson), or broken off (they may be present in the bottom of the sample). Be careful, since several species (and genera) may be present in the same sample. The uropod basal part is the **peduncle**; from this projects one or two branches. The lateral branch is the **lateral ramus**, which is only rarely absent, otherwise it is always longer than the medial branch, called the **medial ramus**. The exopod may be of one or two articles, endopod of only one or is absent. Note that sometimes the articulation between articles 1 and 2 is difficult to see; note also that sometimes article 2 is shorter than and hidden between apical spines of article 1.

A remarkable number of amphipods are troglobionts. Many species, entire genera and even some families are troglobiotic. They are generally troglomorphic (i.e., without pigmentation and eyes, and with elongated legs). Note that "eyes absent" in this key means the lack of black eye pigmentation (not necessarily a lack of the vision elements); also note that yellow specks at the eye location are not reduced eyes. We very often encounter troglobiotic amphipods in springs and wells. In *Niphargus*, all epigean species are eyeless also.

MATERIAL PREPARATION AND PRESERVATION

Amphipods are best preserved and examined in ethanol. It is essential that the first lot of preservative or fixative be replaced after some 10 min, in order to prevent dilution by body fluids or water present in any debris collected with the animals. A preservative of 70% ethanol with some glycerol added is the best for morphological examination. Use 95% ethanol for material to be used in molecular analyses.

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KEYS TO AMPHIPODA

These keys are broken into three separate sets. The first keys include all Palearctic inland aquatic amphipod genera (freshwater, brackish, and most amphibious and marine taxa that occur under freshwater influence), except the endemic genera of the Ponto-Caspian region and Lake Baikal. A separate key is presented for the Ponto-Caspian genera represented within the Caspian Sea and the associated estuaries and limans (lagoons) around Caspian and the Black Sea. Marine taxa in the Black Sea are not treated. A separate key is presented for the endemic taxa of Lake Baikal.

Malacostraca: Amphipoda: Gammaroidea: Families

Ponto-Caspian region (see page 849) and Lake Baikal (see page 852) endemic taxa are treated separately.

1 Body cylindrical, vermiform, pleonites without epimera; pereopodal coxae minute, not widened into plates; gnathopods with enlarged article 5, finger biarticulate of articles 6 + 7; pleopods somehow reduced; troglobiotic; superfamily Ingolfiellidea 2

1′ Body not explicitly vermiform; coxae enlarged into plates, pleonal epimera developed; gnathopods with enlarged article 6, dactylus is article 7 3

2(1)	Pleopods shaped as small, uniarticulate lamellae; brackish, freshwater or marine ..... Ingolfiellidae, one genus: *Ingolfiella* [Southern Europe]
2′	Pleopods bacilliform, with 1−2 articulate rami; freshwater ..... Metaingolfiellidae, one genus: *Metaingolfiella* [Italy]
3(1)	Head with an obvious rostrum 4
3′	No rostrum or rostrum length is less than 20% (one-fifth) of the entire head length 6
4(3)	Eyes well developed; uropod III rami subequal, exopodite of one article 5
4′	Eyes absent; uropod III exopodite of two articles, endopodite scaliform, freshwater ..... **Niphargidae** (in part) [Croatia]
5(4)	Eyes lateral; pereon and pleon with a dorsomedial row of posteriorly pointed keels; uropod III rami foliaceous, bordered by dense setal row; antenna I longer than II, freshwater, brackish, and marine ..... Gammaracanthidae, one genus: *Gammaracanthus* [northern Eurasia]
5′	Eyes dorsal; body without a median series of keels; uropod III rami lanceolate, narrowly pointed, poorly setose; antenna I shorter than II ..... **Oedicerotidae [p. 843]**
6(3)	Pereon or pleon with paired lateral projections 7
6′	Pereon or pleon without lateral projections 9
7(6)	Uropod III endopodite length not less than one-third of exopodite length, both rami richly setose; pereopodal coxae with lateral projections; body ca 10 mm or more in length 8
7′	Uropod III endopodite scaliform, exopodite with few setae; pereonites with lateral projections; body less than 5 mm long ..... ? Anisogammaridae, one genus: *Fuxiana* [China, Yunnan]
8(7)	Northern Palaearctic ..... Pallaseidae (in part), *Pallasea*
8′	Kyrgyzstan (Lake Ysyk Köl) ..... Gammaridae (in part); *Issykogammarus hamatus* Chevreux, 1908
9(6)	Pleon either smooth, or with sole median projections, or with more than two small denticles 10
9′	Pleonites with one pair of dorsal projections each, jutting or adhering to dorsum, rarely absent ..... **Gammaridae** (in part)
10(9)	Urosoma not as below 11
10′	Urosoma basically developed normally, cylindrical or conical, dorsally with spines and/or setae, or with dorsal elevations, projections or keels 13
11(10)	Urosoma dorsally flat, entire body slightly depressed; antenna I shorter than II; epigean animals (superfamily Corophioidea) 12
11′	Urosomite I enlarged, dorsally carinate, hiding urosomites II and III; antenna I longer than II; uropod III exopodite of one article, hardly longer than the globular sympodite, enopodite absent, with some spines, no setae; gnathopod I and II palmar inclination ca 90°; no eyes; interstitial animals ..... **Niphargidae** (in part)
12(11)	Urosomites I and II fused (but III free); gnathopod II with articles 4 and 5 attached in ordinary fashion, perimarine ..... Kamakidae [Eastern Palaearctic]
12′	All urosomites free or all urosomites fused ..... **Corophioidea [p. 846]**
13(10)	Antenna I without accessory flagellum; antenna I not more than 80% of antenna II length; mandibular palp vestigial or absent; maxilla I palp vestigial or absent; uropod III with one or no rami (rarely with a small endopodite), ramus barely longer than sympodite (superfamily Talitroidea) 14
13′	Antenna I with accessory flagellum of one to several tiny bacilliform articles (in Eusiridae in Far East may be vestigial, but still present); uropods variously developed 17
14(13)	Antenna II and pereopods V−VII not heavily setose and spinose 15
14′	Antenna II peduncle heavily setose; pereopods V−VII heavily setose and spinose ..... **Dogielinotidae [p. 846]**
15(14)	Maxilliped palp with dactylus anguiform; gnathopod II (both sexes) subchelate 16
15′	Maxilliped palp with dactylus vestigial or absent; gnathopod II (female) minutely chelate; pereopods V−VII not heavily setose ..... **Talitridae [p. 846]**
16(15)	Maxilla I palp with two articles; uropod III with minute endopodite; telson cleft ..... Hyalidae, one genus: *Parallorchestes* [Japan, Russia (Okhotsk Sea, Bering Sea) Nearctic]
16′	Maxilla I palp with single article; upopod III without endopodite; sternal gills present; telson entire ..... Hyalellidae, one genus: *Hyalella* [Nearctic, Neotropical. Potentially introduced to Palaearctic]
17(13)	Gills without accessory lobes 18

17′ Most gills with subcylindrical accessory lobes; male gnathopod palm with blunt spines ..... **Anisogammaridae [p. 847]**

18(17) Uropod III with at least one ramus (exopodite) 19

18′ Uropod III without rami, sympodite not longer than telson; pereopod dactyli with several posterior setae; telson entire or shallowly cleft; urosomites fused ..... Crangonyctidae (in part): *Lyurella* [Azerbaijan, Georgia, Russia (between Black Sea and Caspian Sea)]

19(18) Uropod III with exopodite only, if endopodite is present, it is vestigial (less than 10% sympodite length) 20

19′ Uropod III with both rami (endopodite may be small, but not vestigial) 24

20(19) Uropod III small and broad, its length not twice its sympodite width, exopodite length not more than twice its basal width; pereopod VII basis (article 2) broad, not twice as long as wide, or with a remarkable distoposterior lobe (in *Parasalentinella*) 21

20′ Uropod III longer, at least three times as long as sympodite width; pereopod VII article 2 (base) narrow, its length more than twice the width, without a distoposterior lobe; eyes absent or rudimentary ..... **Pseudocrangonyctidae [p. 848]**

21(20) Uropod I longer than II, reaching close to or beyond its apex 22

21′ Uropod I shorter, reaching only the base of uropod II; telson entire, wider than long; antenna I article 1, distal border dorsally extended; mandibular palp well developed, but its distal article not reaching 30% of article 2 length; eyes absent; interstitial .... Salentinellidae (in part): *Parasalentinella* [France]

22(21) Urosome clearly segmented; telson entire; eyes absent 23

22′ Urosomites fused; telson cleft up to 30% its length; mandibular palp normally developed; uropod III with no trace of endopodite; with sternal gills; eyes developed or reduced ..... Crangonyctidae (in part): *Synurella*

23(22) Mandibular palp vestigial; uropod III may have a vestigial endopodite ..... **Metacrangonyctidae [p. 848]**

23′ Mandibular palp normal ..... Crangonyctidae (in part): *Stygobromus* [Central and eastern Palaearctic. Nearctic]

24(19) Below two character states not both present 25

24′ Pereopod VII article 2 (basis) with a very large, nearly circular posterior lobe, article longer than the rest of appendage; uropod III endopodite more than 75% exopodite length ..... **Pontoporeiidae** (in part)

25(24) Uropod III, with rami subequal, uniarticulate, not densely setose 26

25′ Uropod III endopodite 90% exopodite length or shorter, to scaliform, if rami appear subequal, the margins are densely setose; uropod III exopodite of two articles, or of one article with group of terminal spines 28

26(25) Uropod III rami flat and lanceolate, ending in a narrowly sharp point without apical spine group 27

26′ Uropod III rami bacilliform, apically with a group of spines and/or setae; pereopod VII article 2 (base) narrow, at least twice as long as wide; tiny troglobiotic ..... **Bogidiellidae [p. 848]**

27(26) Antenna I accessory flagellum article bacilliform; mandibular molar weak, not triturative; maxilla I normally developed; only pedunculate coxal gills, sternal gills absent; uropod III rami without series of plumose setae; eyes absent .... Lucioblividae, one genus: *Lucioblivio* [Japan]

27′ Antenna I accessory flagellum vestigial, hardly longer than wide; mandibular molar normally developed, triturative .... **Pontogeneiidae [p. 849]**

28(25) Uropod III exopodite article 2 shorter than 30% the length of article 1 or absent 29

28′ Uropod III exopodite article 2 longer than 30% the length of article 1 30

29(28) Pereopod III (but not IV) with articles 4–6 posterior surface lacking a setal brush 35

29′ Pereopod III (but not IV) with articles 4–6 posterior surface with a dense setal brush; uropod III exopodite article 2 vestigial or absent ..... **Gammaridae** (in part) [Central Asia]

30(29) Uropod III endopodite short, scaliform 31

30′ Uropod III flat or strongly elongate, endopodite longer than 50% of exopodite article 1; eyes absent; coastal, interstitial .... Eriopisidae, one genus: *Psammogammarus* [Mediterranean]

31(30) Uropod III without plumose setae; eyes absent 32

31′ Uropod III exopodite with a marginal row of long plumose setae; eyes present ..... **Gammaridae** (in part) [SE Europe]

32(31) Pereopod VII article 4 without a broad posterior lobe 33

32′ Pereopod VII article 4 with a broad posterior lobe, not twice as long as broad; brackish, interstitial ..... Eriopisidae, one genus: *Victoriopisa* [Mauretania. Oriental]

33(32) Gnathopod I without a distoposteriorly directed, massive bulge 34

33′ Gnathopod I article 5 with a distoposteriorly directed, massive bulge ..... **Niphargidae** (in part) [Western Europe]

34(33) Maxilla I palps asymmetrical, medial lobe with an apical row of setae ..... **Gammaridae** (in part) [Central Asia]

34′ Maxilla I palps symmetrical, medial lobe with one or several bunched apical setae; maxilla II without a facial row of setae ..... **Niphargidae** (in part) [Europe, Middle East]

35(29) Gnathopod I propodus 160% as long as propodus II or longer; uropod III endopodite long to scaliform, and less than 50% exopodite length 36

35′ Gnathopod I propodus less than 150% or smaller than propodus II 37

36(35) Pereopod VII base narrow, tapering distad, dactylus normal ..... Eulimnogammaridae, one genus: *Iberogammarus* [Europe]

36′ Pereopod VII base wide and rounded, with a large distoposterior lobe ..... Iphigenellidae, one genus: *Iphigenella* [SE Europe. Oriental]

37(35) Uropod III endopodite at least as long as exopodite article 1, article two present, if marginal setae are present, they are only single and adjacent to spines; maxilla II without facial setae row 38

37′ Uropod III either with endopodite shorter than exopodite, or with dense, marginal plumose setae at least along one side of each ramus 39

38(37) Gnathopod II palm more oblique than palm I; eyes absent; troglobiotic ..... **Hadziidae** [Southern Europe]

38′ Gnathopod I palm stronger inclined than palm II; eyes present; brackish ..... **Mesogammaridae** (in part) [Eastern Palaearctic]

39(37) Pereopod VII article 2 not as below 40

39′ Pereopod VII article 2 semicircular, strongly widened medially, but without a posteriodistal lobe, and posterior margin with a dense row of long setae; uropod III without article 2 ..... Micruropodidae (in part): *Micruropus* [E Europe, N Asia]

40(39) Pereopod III without a dense brush of long setae, or both pereopod III and IV articles 4 and 5(6) posterior margins with a dense brush of long setae; peri-Mediterranean and Atlantic regions 41

40′ Pereopod III (but never pereopod IV) articles 4 and 5(6) posterior margins with a dense brush of long setae; if such a brush also on pereopod IV, then material is from Central Asia; fresh and brackish water ..... **Gammaridae** (in part) [Atlantic islands, peri-Mediterranean, Central Asia]

41(40) Uropod III exopodite article two absent 42

41′ Uropod III exopodite article 2 present, although sometimes shorter than apical spines and hidden between them 53

42(41) Uropod III exopodite at least twice as long as wide; maxilla I palp normal, of three articles 43

42′ Uropod III exopodite less than twice as long as wide, endopodite scaliform, shorter than sympodite; maxilla I palp vestigial of one article ..... **Niphargidae** (in part) [Slovenia]

43(42) Uropod III endopodite shorter than 30% exopodite length, mainly scaliform 44

43′ Uropod III endopodite longer than 30% exopodite length; eyes absent ..... **Gammaridae** (in part)

44(43) Maxilla I medial lobe with one or more apical setae in a tuft; maxilla II without a facial line of strong setae 45

44′ Maxilla I medial lobe with two or more setae in an apical or lateral row; maxilla II usually with a facial oblique to longitudinal setal row 48

45(44) Gnathopod II article 5 without a digitiform projection, rounded triangular, posterodistally with setae; maxilla II with more than 10 apical setae 46

45′ Gnathopod II article 5 with a digitiform projection, posterodistally without setae; mandibular palp article 3 with ca five setae only; maxilla II lobes only with ca 3 and 5 apical setae ..... ? Niphargidae, one genus: *Crangonyx paxi* [Central Europe]

46(45) Uropod III exopodite bacilliform, more than twice as long as sympodite 47

46′ Uropod III exopodite aciculate, less than twice length of sympodite; telson not incised ..... Pseudoniphargidae (in part): *Parapseudoniphargus* [Spain]

47(46) Telson entire or with a shallow (less than one-third length) apical concavity ..... Pseudoniphargidae (in part): *Pseudoniphargus* [Peri-Mediterranean, Atlantic islands]

47′ Telson incised more than one-half length ..... **Niphargidae** (in part) [Iberian Peninsula]

48(47) Maxilla I lateral lobe with ca 10 or fewer serrated spines 49

48′ Maxilla I lateral lobe with ca 20 serrate spines, palp reaching spine bases; pereopod VII base with posterior margin sinuate, broad proximally and narrow distally [W Caucasus] ..... **Gammaridae** (in part)

49(48) Telson cleft 60% or deeper; sternal gills absent; gnathopod II palmar margin with only setae and few spines 50

49′ Telson entire to less than 50% incised; sternal gills present; gnathopod II palm with a series of short spines ..... Crangonyctidae (in part): *Crangonyx* [Holarctic]

50(49) Maxilla II without facial longitudinal row of setae 51

50′ Maxilla II with a facial oblique to longitudinal setal row ..... **Mesogammaridae** (in part) [Japan, Korea]

51(50) Mandibular palp normal, of three articles 52

51′ Mandibular palp vestigial; maxilla II without facial row of setae ..... Melitidae (in part): *Phreatomelita* [Iran]

52(51) Uropod I not reaching tip of uropod II or beyond; maxilla II without facial row of setae; eyes present; perimarine ..... Melitidae (in part): *Melita* [Holarctic, Caspian Sea]

52′ Uropod I not reaching tip of uropod II (probably in *T. setiferus* longer); maxilla II with obliquely longitudinal setal row; eyes absent ..... **Gammaridae** (in part) [Central Asia]

53(41) Uropod III endopodite scaliform, not longer than exopodite width (rarely up to 150% (1.5) of its width) 54

53′ Uropod III endopodite longer, 20% (one-fifth) to 100% of exopodite length 59

54(53) Uropod III not as below; gnathopod II article 6 enlarged, forming subchela with dactylus 55

54′ Uropod III exopodite margined on one side with very long (more than twice exp width) plumose setae; gnathopod II article 6 reduced, without subchela, dactylus absent; brackish ..... **Pontoporeiidae** (in part) [Perimarine]

55(54) Pereopod VII base not as below 56

55′ Pereopod VII article 2 expanded, unlobate ventrally, densely setose posteriorly ..... Micruropodidae (in part): *Gmelinoides* [Baikal. Introduced elsewhere]

56(55) Pereopod VII base width greater than one-third of its length; pereopod dactylus with only few internal spines 57

56′ Pereopod VII base (art. 2) narrow, its width ca 30% (one-third) of its length, both margins straight and parallel; pereopod VII dactylus with ca 10 medial spines; freshwater ..... Crymostygiidae, one genus: *Crymostygius* [Iceland]

57(56) Urosomites without noticeable projections 58

57′ Urosomites I and II with mediodorsal knobs or cones with some apical spines ..... **Gammaridae** (in part)

58(57) Maxilla I medial lobe with two or more setae in an apical or lateral row; maxilla II mainly with a facial row of strong setae ..... **Gammaridae** (in part)

58′ Maxilla I medial lobe with one or more apical setae in a cluster; maxilla II without a facial longitudinal row of setae; fresh and brackish water ..... **Niphargidae** (in part) [Europe, Middle East]

59(53) Uropod III setae different and differently disposed than described below 60

59′ Uropod III with marginal spines along one or both rami, and with single plumose seta ..... **Mesogammaridae** (in part) [Japan]

60(59) Pereopod VII article 2 face usually glabrous, seldom with irregularly spaced setae 61

60′ Pereopod VII article 2 with several groups of long setae; fresh and brackish water ..... **Gammaridae** (in part) [Europe, W Asia]

61(60) Antenna I longer than or equal to II; maxilla I medial lobe with row of lateral setae 62

61′	Antenna I only ca 75% (three-quarters) length of antenna II; maxilla I medial lobe with one apical seta; maxilla II without facial row of setae; eyes absent; freshwater ..... Sensonatoridae, one genus: *Sensonator* [Spain]
62(61)	Pereopod VII base (art. 2) without posteriodistal lobe or lobe is rounded (angulate in *Gammarus gauthieri*, Morocco, which has eyes present) 63
62′	Pereopod VII base (art. 2) posteriodistal lobe sharply angulate; uropod III endopodite longer than 75% (three-quarters) of exopodite; eyes absent; freshwater karst ..... **Gammaridae** (in part) [Dinaric Alps]
63(62)	Pereopod VII base (art. 2) with posteriodistal lobe small or lacking; maxilla II with facial oblique-longitudinal setal row 64
63′	Pereopod VII base (art. 2) with a large posteriodistal lobe; maxilla II without facial longitudinal setal row; eyes absent ..... **Gammaridae** (in part)
64(63)	Gnathopod II subchelate, palm margin inclination less than 60°; mandibular palp article 3 shorter than 50% (one-half) of article 2, without a regular comblike row of setae; eyes absent; fresh and brackish water ..... Salentinellidae (in part): *Salentinella* [Northern Peri-Mediterranean]
64′	Gnathopod II chelate, palm margin inclination greater than 100°; mandibular palp article 3 longer than 50% (one-half) of article 2, with a marginal comb of strong setae; fresh and ? brackish water ..... **Niphargidae** (in part)

Amphipoda: Niphargidae: Genera

Members of this family lack eyes, the maxilla I medial lobe has several setae in an apical cluster, and maxilla II lacks a facial longitudinal setal row. Niphargids occur in fresh (possibly brackish) water and are found in Europe and the Middle East.

1	Urosoma normally segmented 2
1′	Urosomite I enlarged, dorsally carinate, hiding urosomites II and III; antenna I longer than II; uropod III exopodite of one article, hardly longer than the globular sympodite, enopodite absent, with some spines, no setae; gnathopods I and II palm margin inclination ca 90°; interstitial animals ..... *Carinurella* [Italy, Slovenia]
2(1)	Uropod III endopodite scaliform, if elongate, both exopodite articles are bacilliform 3
2′	Uropod III endopodite 50% or more exopodite length, exopodite flat ..... *Pontoniphargus* [Romania]
3(2)	Uropod III exopodite of one article 4
3′	Uropod III exopodite of two articles 5
4(3)	Uropod III exopodite cylindrical, twice as long as its terminal spines; maxilla I palp vestigial, of one article ..... *Niphargobates* [Slovenia]
4′	Uropod III exopodite bacilliform, several times longer than sympodite; maxilla I normal ..... *Haploginglymus* [Portugal, Spain]
5(3)	Mandibular palp article 3 with five or fewer setae 6
5′	Mandibular palp article 3 with a normal setal comb 7
6(5)	Gnathopod I article 5 with a posteriodistally directed, massive bulge, article 6 elongated ..... *Microniphargus* [Western Europe]
6′	Gnathopod I article 5 without such bulge, article 6 triangular ..... *Niphargellus* [Central Europe]
7(5)	Maxilla I lateral lobe with several tens of spines ..... *Niphargopsis* [Central and Eastern Europe]
7′	Maxilla I with approximately 10 spines ..... *Niphargus* [Europe and Middle East]

Amphipoda: Oedicerotidae: Genera

Three genera from the Yenisei Gulf area of Russia.

1	Eyes in contact dorsomedially; dorsum smooth 2
1′	Eyes divided by a ridge (crest); rostrum longer than 60% (two-thirds) of head; entire body dorsally multicarinate (paired + median projections) ..... *Acanthostepheia*

2(1)	Gnathopod I propodus shorter and thicker than gnathopod II propodus; gnathopod I article 5 with protuberance long, reaching the end of article 6 ..... *Deflexilodes*
2′	Gnathopods I and II with propodus equally large; protuberance of gnathopod I article 5 short, not reaching the end of article 6 ..... *Oediceros*

Amphipoda: Gammaridae: Genera

1	Pereon without lateral projections 2
1′	Pereon with paired lateral projections; uropod III endopodite length more than half exopodite length, both rami richly setose; pereopodal coxae with lateral projections; body ca 10 mm in length ..... *Issykogammarus* [Kyrgyzstan (Lake Ysyk Köl)]
2(1)	Pleon either smooth, or with sole median projections, or with more than two small denticles 3
2′	Pleonites with one pair of dorsal projections each, jutting or adhering to dorsum, rarely absent; eyes absent ..... *Metohia* (in part) [Dinaric Alps]
3(2)	Uropod III exopodite article 2 shorter than 30% the length of article 1 or absent 4
3′	Uropod III exopodite article 2 longer than 30% the length of article 1 5
4(3)	Pereopod III (but not IV) with articles 4−6 posterior surface lacking a setal brush 6
4′	Pereopod III (but not IV) with articles 4−6 posterior surface with a dense setal brush; uropod III exopodite article 2 vestigial or absent ..... *Sarothrogammarus* [Central Asia]
5(3)	Uropod III without plumose setae; eyes absent; Gnathopod I without a posteriodistally directed, massive bulge; maxilla I palps asymmetrical, medial lobe with an apical row of setae 9
5′	Uropod III exopodite with a marginal row of long plumose setae; eyes present ..... *Stenogammarus* [SE Europe]
6(4)	Pereopod III without a dense brush of long setae, or both pereopod III and IV articles 4 and 5(6) posterior margins with a dense brush of long setae; peri-Mediterranean and Atlantic regions 7
6′	Pereopod III (but never pereopod IV) articles 4 and 5(6) posterior margins with a dense brush of long setae; if such a brush also on pereopod IV, then material is from Central Asia; fresh and brackish water ..... 9 [Atlantic islands, peri-Mediterranean, Central Asia]
7(6)	Uropod III exopodite article 2 absent; 8
7′	Uropod III exopodite article 2 present, although sometimes shorter than apical spines and hidden between them 18
8(7)	Maxilla I lateral lobe with ca 10 or fewer serrated spines; uropod I not reaching tip of uropod II (probably in *T. setiferus* longer); maxilla II with obliquely longitudinal setal row; eyes absent; *Sarothrogammarus* group genera ..... 9 [Central Asia]
8′	Maxilla I lateral lobe with ca 20 serrate spines, palp reaching spine bases; pereopod VII base with posterior margin sinuate, broad proximally and narrow distally [West Caucasus] 15
9(8)	Pereopod III articles 4(6) posteriorly with a dense setal brush 10
9′	Pereopods III and IV without posterior dense setal brushes ..... *Tadzocrangonyx* [Central Asia]
10(9)	Only pereopod III with a brush, pereopod IV with shorter and sparser setation 11
10′	Pereopod IV also posteriorly with a dense setal brush ..... *Comatogammarus* [Tajikistan]
11(12)	Uropod I reduced, not reaching apices of uropod II, rami without dorsal spines 12
11′	Uropod I rami with dorsal spines 13
12(11)	Maxilla I lobes widened, all spines densely pectinate; pereopod VII elongated, base (art. 2) more than twice as long as wide; brackish ..... *Longigammarus* [Ligurian Sea coast]
12′	Maxilla I normal, not all spines pectinate; pereopod VII base ca twice as long as wide; fresh and brackish water ..... *Rhipidogammarus* [Peri-Mediterranean, Atlantic islands]
13(11)	Uropod I longer than II and reaching its apex 14
13′	Uropod I longer than II, but not reaching its apex; fresh and ?brackish water ..... *Tyrrhenogammarus* [Mediterranean islands]

14(13) Male gnathopod 2 palm margin straight to slightly concave; freshwater ..... *Sarothrogammarus* [Central Asia]

14′ Male gnathopod 2 palm margin concave, without midpalmar spine; fresh and ?brackish water ..... *Lusigammarus* [Atlantic islands]

15(8) Male uropods with setae arranged differently than below 16

15′ Male uropods I–III with bunches of very long setae; maxilla I lateral lobe with more than 15 serrated spines ..... *Adaugammarus* [Caucasus]

16(15) Maxilla I outer lobe with ca 10 serrate spines in a double row; freshwater, Dinaric karst 17

16′ Maxilla I lateral lobe with ca 100 serrate spines in several rows ..... *Zenkevitchia* [Caucasus]

17(16) Maxilla I palp reaching bases of serrate spines, middle spines with over 40 denticles; pereopod VII article 2 broad, its width ca 70% of length ..... *Accubogammarus* [Croatia, ? Montenegro]

17′ Maxilla I palp reaching apices of serrate spines, middle spines with ca 20 denticles; pereopod VII article 2 narrow, its width ca 75% of length ..... *Typhlogammarus* [Croatia, Hercegovina, Montenegro]

18(7) Uropod III endopodite scaliform, not longer than exopodite width (rarely up to 150% (1.5) of its width) 19

18′ Uropod III endopodite longer, 20% (one-fifth) to 100% of exopodite length 33

19(18) Urosomites I and II with mediodorsal knobs or cones with some apical spines 20

19′ Urosomites without noticeable projections 21

20(19) Pereopods I and VII coxae margins strongly setose; fresh and brackish water ..... *Turcogammarus* [Central Eurasia]

20′ Pereopods I–VII coxae with short, sparse setae; fresh and brackish water ..... *Dikerogammarus* [Europe, Western Asia. Invasive]

21(19) Pereopod VII base (art. 2) distal one-third or more tapering, posterior margin straight; without a posteriodistal lobe 22

21′ Pereopod VII base (art. 2) posterior margin rounded or at least slightly convex, often with a posteriodistal lobe 27

22(21) Maxilla I asymmetrical, palp longer than spines 23

22′ Maxilla I symmetrical, palp not reaching spine apices; antenna I accessory flagellum of one article; freshwater ..... *Gammarus* (= *Fontogammarus*) [Southeastern Europe (Central Dinaric Alps)]

23(22) Uropod III setation diverse, but always straight (note: the following genera are very difficult to distinguish morphologically but are strongly supported molecularly) 24

23′ Uropod III exopodite margins with dense, long, curled setae; fresh and brackish water ..... *Trichogammarus* [Ponto-Caspian. Invasive elsewhere]

24(25) Telson lobes each less than twice as long as wide 25

24′ Telson lobes each at least twice as long as wide (Atlantic) 26

25(24) Uropod III setae longer and denser than marginal spines (some exceptions in Spain and N Africa); telson lobes ca 1.5 times as long as wide; fresh and brackish water ..... *Homoeogammarus* [Peri-Mediterranean, ?Peri-Atlantic]

25′ Uropod III setae shorter than exopodite width and sparser than marginal spines; telson lobes hardly longer than wide; fresh and brackish water ..... *Chaetogammarus* [Black Sea. Invasive elsewhere]

26(24) Uropod III with setae longer than spines, at least on one side; brackish to marine ..... *Marinogammarus* [Peri-Atlantic]

26′ Uropod III without setae; ?brackish water, marine ..... *Relictogammarus* [Atlantic]

27(21) Dorsum lacking a keel 28

27′ Pleonites and some pereonites with mediodorsal keels (not pointed); pereopod VII base with a large posteriodistal lobe; fresh and brackish water ..... *Amathillina* [Eastern Europe, Western Asia]

28(27) Uropod III bearing a fan of dense, long marginal setae; pereopod VII basal article (art. 2) face with setae in groups 29

28′ Uropod III with setae only with marginal spines, or absent 30

29(28) Pereopod IV article 4, posterior setae divided into groups; fresh and brackish water ..... *Obesogammarus* [Ponto-Caspian. Invasive in Europe]

29′ Pereopod IV article 4, posterior setae arranged in a continuous fan; fresh and brackish water ..... *Pontogammarus* [Ponto-Caspian. Invasive in Europe]

30(28) Pereopod VII base (art. 2) with a distinct posteriodistal lobe 31

30′ Pereopod VII base (art. 2) without a posteriodistal lobe; uropod III without setae; ?brackish and marine ..... *Relictogammarus* [Atlantic]

31(30) Uropod III with either only a few or very short setae; pereopod VII base with a broad and rounded posteriodistal lobe 32

31′ Uropod III with several long, plumose setae joined with marginal spines; pereopod VII with small, rounded-triangular posteriodistal lobe; fresh to ?brackish water ..... *Ilvanella* [Italy]

32(31) Antenna I accessory flagellum of a single article; both gnathopods subequal in size ..... *Jugogammarus* [Slovenia]

32′ Antenna I accessory flagellum with three articles or more; gnathopod II distinctly stouter than I; fresh and brackish water ..... *Shablogammarus* [Central Eurasia]

33(18) Pereopod VII article 2 face usually glabrous, seldom with irregularly spaced setae 34

33′ Pereopod VII article 2 with several groups of long setae; fresh and brackish water ..... *Pontogammarus* [Europe, W Asia]

34(33) Pereopod VII base (art. 2) without posteriodistal lobe or lobe is rounded (angulate in *Gammarus gauthieri*, Morocco, which has eyes) 35

34′ Pereopod VII base (art. 2) posteriodistal lobe sharply angulate; uropod III endopodite longer than 75% (three-quarters) of exopodite; eyes absent; freshwater karst ..... *Metohia* (in part) [Dinaric Alps]

35(34) Uropod III endopodite 40% exopodite length or longer 36

35′ Uropod III endopodite 30% exopodite length or shorter 38

36(35) Maxilla I lateral lobe with less than 15 straight spines 37

36′ Maxilla I lateral lobe with 17 curved spines; coxal gill VII absent ..... *Albanogammarus* [Albania]

37(36) Maxilla I lateral lobe with 11 or more spines; eyes absent ..... *Anopogammarus* [Caucasus]

37′ Maxilla I lateral lobe with ca 10 spines; freshwater, brackish, and marine ..... *Gammarus* [Holarctic]

38(35) Maxilla I lateral lobe with ca 10 spines; southwestern Europe 39

38′ Maxilla I lateral lobe with 12 or more spines; eyes absent ..... *Anopogammarus* [Caucasus area]

39(38) Freshwater ..... *Parhomoeogammarus* [France, ?Spain]

39′ Marine ..... *Marinogammarus* [Atlantic]

Amphipoda: Corophioidea: Families and Genera

Members of this family have the urosome flattened dorsally, with the entire body slightly depressed, and antenna I shorter than II.

1 All urosomites free ..... (Corophiidae) 2

1′ Some or all urosomites fused 3

2(1) Antenna II article 2 with gland cone large, conspicuous; uropod III ramus short, broad, little longer than peduncle; brackish to marine ..... *Corophium* [Perimarine]

2′ Antenna II article 2 with gland cone small to medium, not prominent; uropods I and II, rami with medial spines (setae); antenna II powerful, similar in both sexes, article 4 and flagellum short; freshwater, brackish, and marine ..... *Chelicorophium* [Western Palearctic, Ponto-Caspian]

3(1) Urosomites I and II fused (but III free); gnathopod II with articles 4 and 5 attached in ordinary fashion; freshwater, brackish, and marine ..... Kamakidae, one genus: *Kamaka* [Far East, perimarine]

3′ All urosomites fused; brackish to marine ..... Corophiidae: *Monocorophium* [Perimarine]

Amphipoda: Dogielinotidae: Genera

1 Uropod III with ramus; pereopods III and IV with article 4 lacking an anterodorsal lobe, pereopod VI article 5 slender; pleonal epimera III weakly pointed posteroventrally; marine to brackish ..... *Dogielinotus* [Japan, Russia (Kuril Islands, Okhotsk Sea)]

1′ Uropod III without ramus; pereopods III and IV with article 4 with sharp anterodorsal lobe, pereopod VI article 5 variously expanded; pleonal epimera III with large posteroventral tooth; telson weakly cleft; marine to brackish ..... *Haustorioides* [Japan, Russia (Kuril Islands, Okhotsk Sea)]

Amphipoda: Talitridae: Genera

Family characterized by the antenna I accessory flagellum absent, the mandibular palp absent, and uropod III either uniramous (except in *Parallorchestes* and *Parhyale*, neither is treated here) or without rami.

1 Male gnathopod I distinctly subchelate, palm transverse, articles 5 and 6 (occasionally article 4 also) with broad pellucid lobe; female gnathopod I weakly subchelate, palm oblique or vertical, shorter than dactylus, articles 5 and 6 without pellucid lobe 2

1′ Gnathopod I (both sexes) weakly subchelate to simple, or distinctly subchelate 7

2(1) Male gnathopod I articles 5 and 6 each with a pellucid lobe 3

2′ Male gnathopod I articles 4–6 with pellucid lobe; moist places near freshwater or brackish water ..... *Cryptorchestia* [Peri-Atlantic, peri-Mediterranean]

3(2) Uropod I exopodite with margin spinose 4

3′ Uropod I exopodite with margin glabrous; marine supralittoral, freshwater margins, terrestrial (Fig. 16.6.24) ..... *Platorchestia* [Atlantic Coasts. Nearctic, Oceana]

4(3) Oostegite setae apically simple 5

4′ Oostegite setae apically curled; marine supralittoral, estuaries, salt marshes ..... (Fig. 16.6.25) ..... *Traskorchestia* [Japan, Russia (Pacific). Nearctic]

5(4) Male pereopod VII article 6 without a setal tuft 6

5′ Male pereopod VII article 6 with a setal tuft; caves, sea shores, estuaries ..... *Macarorchestia* [Atlantic, Mediterranean]

6(5) Pereopod VII (both sexes) article 2 posterior margin evenly rounded; marine supralittoral, brackish, freshwater ..... *Orchestia* [Atlantic, Mediterranean. Nearctic. Australian]

6′ Pereopod VII (both sexes) article 2 posterior margin posterioventrally expanded (especially in male); marine subtidal, supralittoral, brackish lakes, freshwater lakes, coastal grassland (Fig. 16.6.26) ..... *Ditmorchestia* [Japan, Russia (Pacific)]

7(1) Gnathopod I (both sexes) weakly subchelate or simple, articles 5 and 6 pellucid lobe (if present) small, protruding (especially for article 5) 8

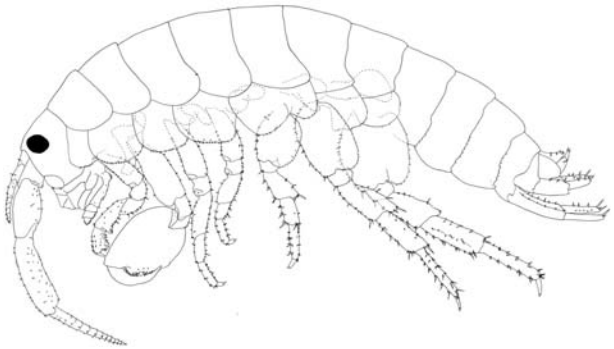


FIGURE 16.6.24 *Platorchestia pacifica* Miyamoto & Morino, 2004. *From Morino (2015).*

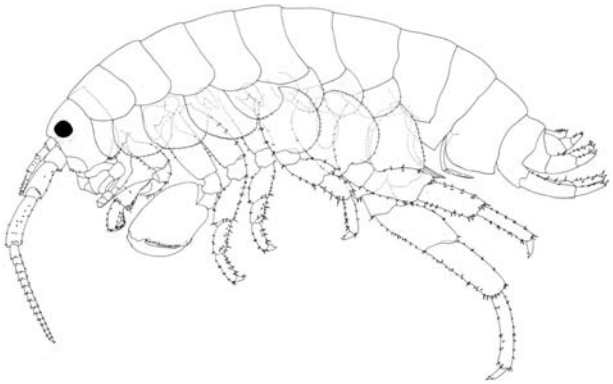


FIGURE 16.6.25 *Traskorchestia ochotensis* (Brandt, 1851). *From Morino (2015).*

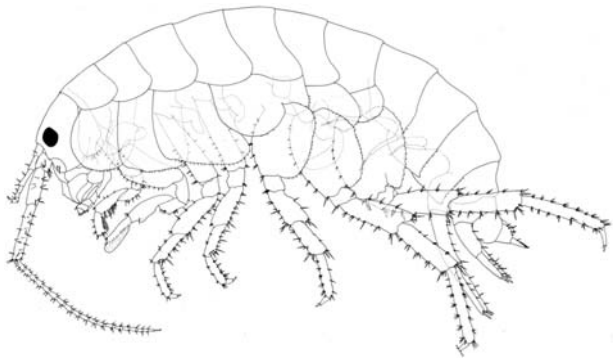


FIGURE 16.6.27 *Pyatakovestia pyatakovi* (Derzhavin, 1923). *From Morino (2015).*

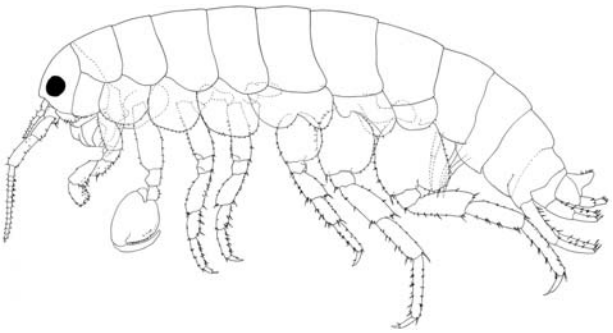


FIGURE 16.6.26 *Ditmorchestia ditmari* (Derzhavin, 1923). *From Morino (2015).*

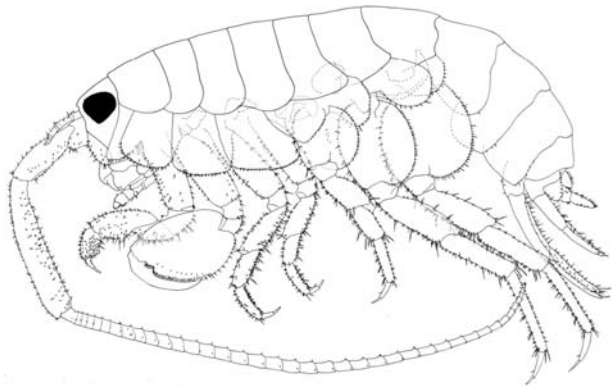


FIGURE 16.6.28 *Trinorchestia trinitatis* (Derzhavin, 1937). *From Morino (2015).*

7′	Gnathopod I (both sexes) deeply subchelate, palm transverse, articles 4–6 with pellucid lobe, articles 5 and 6 with lobes broad; maxilliped precoxa lateral margin stepped; marine supralittoral to coastal inland (Fig. 16.6.27) ..... *Pyatakovestia* [Japan, Korea, Kuril Islands]
8(7)	Male gnathopod I article 6 simple or slender (bearing a shallow palm) 9
8′	Male gnathopod I robust (wider than one-half of length); male gnathopod palm shallow, posterior margin with pellucid lobe at midpoint (article 6) or proximally (article 5); female gnathopod article 6 palm very shallow, without lobe; male gnathopod II powerfully subchelate; marine supralittoral (Fig. 16.6.28) ..... *Trinorchestia* [Japan, Russia (Pacific)]
9(8)	Male gnathopod I article 6 slender (less wide than one-half of length), palm shallow, vertical or oblique, articles 5 and 6 posterodistal margin with a pellucid lobe; female article 6 simple, without lobe; male gnathopod II powerfully subchelate 10
9′	Male gnathopod I article 6 simple; gnathopod II (both sexes) minutely chelate; marine supralittoral ..... *Talitrus* [Atlantic, Mediterranean]
10(9)	Pereopods VI and VII dactylus glabrous; pleonites dorsally smooth 11
10′	Pereopods VI and VII dactylus anterior margin setose; male pleonites with dorsal ridges and spines; marine supralittoral, estuaries (Fig. 16.6.29) ..... *Africorchestia* [Southeast Europe, West Africa]
11(10)	Pereopod V dactylus robust, dissimilar to that of pereopod IV 12
11′	Pereopod V dactylus slender, similar to that of pereopod IV; marine supralittoral ..... *Deshayesorchestia* [Atlantic, Mediterranean]
12(11)	Telson longer than wide, 7–10+ spines per lobe; marine beaches ..... *Sardorchestia* [Mediterranean, Nearctic, Neotropical]
12′	Telson as long as wide, three to six spines per lobe; marine beaches (Fig. 16.6.30) ..... *Britorchestia* [Atlantic, Mediterranean]

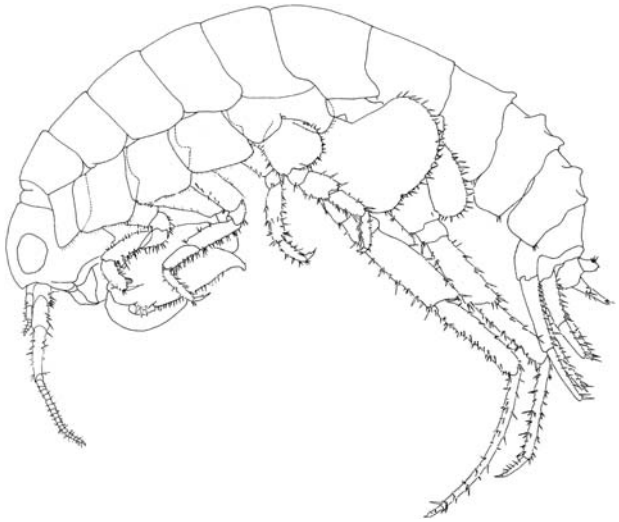


FIGURE 16.6.29 *Africorchestia skoogi* (Stebbing, 1891). *From Lowry and Coleman (2011).*

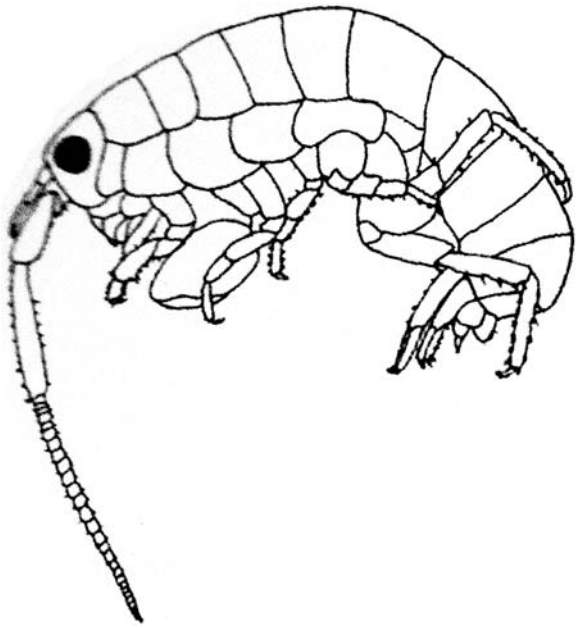


FIGURE 16.6.30 *Britorchestia brito* (Stebbing, 1891). *From Lowry and Bopiah (2012).*

Amphipoda: Anisogammaridae: Genera

Adapted after Barnard & Barnard (1983). This family is characterized by most or all coxal gills with one or more subcylindrical accessory lobes. Occurs in the Far East and Pacific coastal regions.

1	Coxal gills with one or zero accessory lobes 2
1′	Some coxal gills with two or more accessory lobes; middorsal carination of pleonites weak or absent; uropod III exopod with article 2 vestigial or strong 3
2(1)	Uropod III exopodite bacilliform, article 2 hardly longer than surrounding spines, with short setae and spines along both sides; freshwater ..... *Fuxigammaru* [China]

2′	Uropod III exopodite article 1 broad, more than twice as long as wide, with several spines along one side and a row of plumose setae along the other, article 2 longer than spines; freshwater ..... *Eurypodagammarus* [China (Yunnan)]
3(1)	Urosomite 2 never with more than one spine or cusp, tall projections if present bearing only one apical spine, uropod III medial ramus less than half as long as lateral ramus; antenna 1 subequal to or longer than antenna 2; cephalic sinus lacking a notch 4
3′	Urosomite 2 with a tall median projection bearing a pair of small dorsolateral cusps; uropod III rami subequal; antenna 1 shorter than antenna 2; cephalic sinus with a narrow posterior notch; brackish to marine ..... *Anisogammarus* [Peri-Pacific]
4(3)	Uropods 1 and 2 of ordinary length, well exceeding uropod III peduncle apex; uropod III article 2 exopod distinct; uropods 1 and 2 rami with marginal and apical spines 5
4′	Uropods 1 and 2 short, uropod II rami (excluding spines) not exceeding uropod III peduncle apex; uropod III article 2 exopod vestigial; brackish to marine ..... *Locustogammarus* [Boreal Pacific]
5(4)	Coxa VI gill with three accessory lobes 6
5′	Coxa VI gill with one accessory lobe 7
6(5)	Telsonic lobes fused basally 20% of their length; male antenna 2 calceolate; pleonites dorsally inerm and glabrous; freshwater, brackish to marine ..... *Eogammarus* [Peri-Pacific]
6′	Telsonic lobes basal fusion insignificant; male antenna 2 not calceolate; pleonites dorsally setospinose; freshwater, brackish to marine ..... *Spinulogammarus* [Peri-Pacific]
7(5)	Coxal gills II–V with posterior accessory lobe much smaller than anterior accessory lobe; fresh water .... *Annanogammarus* [China, Japan, Korea]
7b	Coxal gills II–V with accessory lobes of equal size (or only anterior one reduced); fresh to brackish water ..... *Jesogammarus* [China, Japan, Korea]

Amphipoda: Pseudocrangonyctidae: Genera

Both genera are from the far eastern Palaearctic.

1	Uropod III exopodite without article 2 ..... *Procrangonyx*
1′	Uropod III exopodite with a small article 2 ..... *Pseudocrangonyx*

Amphipoda: Metacrangonyctidae: Genera

Two subterranean genera from the Mediterranean.

1	Gnathopod II palm concave ..... *Longipodacrangonyx* [Morocco]
1′	Gnathopod palmae straight ..... *Metacrangonyx* [Mediterranean and adjacent regions]

Amphipoda: Pontoporeiidae: Genera

1	Pereopod VII article 2 (basis) with a very large, nearly circular posterior lobe, article longer than the rest of appendage; uropod III endopodite more than 75% exopodite length
1′	Not as above; brackish and marine ..... *Bathyporeia* [Perimarine]
2(1)	Uropod III exopodite with a small, but distinct article 2; urosomite I with a bicuspidate dorsal projection ..... *Pontoporeia* [Holarctic]
2′	Uropod III exopodite with a vestigial, barely visible article 2; urosomite without a projection ..... *Monoporeia* [Holarctic]

Amphipoda: Bogidiellidae: Genera

Characterized by having uropod III with both rami subequal, bacilliform, apically with a group of spines and/or setae. These are small, troglobiotic (interstitial) animals.

1	Uropod I longer than II, its rami with a group of apical spines; maxilla I palp of two articles; mandibular palp article 3 longer than 1 2
1′	Uropod I slightly shorter than II, its rami without any spines or setae, apically acute; maxilla I palp of one article; mandibular palp article 3 shorter than article1; pleopod endopodite of one article, small; marine ..... *Marinobogidiella* [Mediterranean]
2(1)	Pleopods I–III exopodites of three articles, endopodite of one article or absent; gnathopod I article 5 posteriodistal extension distinct, nearly digitiform, article length about 60% of its width (including projection); maxilla I palp of two articles; mandibular palp article 3 longer than article 1..... 3
2′	Pleopods I and II exopodite of five and four articles, respectively, endopodite of one article, with apical setae; gnathopod I article 5 posteriodistal extension not distinct, article length ca 80% of its largest width; brackish to marine ..... *Aurobogidiella* [Italy]
3(2)	Pleopods or uropods with marked sexually dimorphic modifications 4
3′	Pleopods and uropods without marked sexually dimorphic modifications; freshwater ..... *Bogidiella* [Central and southern Europe, north Africa, central Asia. Afrotropical]
4(3)	Sexual dimorphism in uropod II where some males with spines on uropod II ramus/rami modified; pleopods I–III with endopodites absent; fresh to ?brackish ..... *Medigidiella* [Peri-Mediterranean]
4′	Sexual dimorphism in pleopod II with male pleopod II, article 2 with modified spines; telson wider than long or as wide as long; fresh and brackish water ..... *Stygogidiella* [Peri-Mediterranean, Atlantic islands]

Amphipoda: Pontogeneiidae: Genera

This family occurs in the far eastern Palaearctic.

1	Sternal gills present ..... *Awacaris*
1′	Sternal gills absent ..... *Paramoera*

Amphipoda: Hadziidae: Genera

1	Uropods I and II only rarely with several small plumose setae; telson with only several apical spines 2
1′	Uropods I and II with row of ca five plumose setae; setae dorsally on exopodite; with some spines along telson medial margins .... *Parhadzia* [Anatolia]
2(1)	Gnathopod II article 5 expanded posteriorly; mandibular palp article 2 as long as article 1 ..... *Hadzia* [SE Europe]
2′	Gnathopod II article 5 lacking a posterior lobe; mandibular palp article 2 longer than article 1 ..... *Metahadzia* [Peri-Mediterranean, Portugal]

Amphipoda: Mesogammaridae: Genera

1	Uropod III either with endopodite shorter than exopodite, or with dense, marginal plumose setae at least along one side of each ramus 2
1′	Uropod III endopodite at least as long as exopodite article 1, article 2 present, if marginal setae are present, they are only single and adjacent to spines; maxilla II without facial setae row; eyes present; brackish; ..... *Mesogammarus* [Eastern Palaearctic]
2(1)	Uropod III endopodite ca 30% (one-third) exopodite length or shorter ..... *Eoniphargus* [Japan]
2′	Uropod III endopodite ca 60% (two-thirds) exopodite length or longer ..... *Octopupilla* [Japan]

PONTO-CASPIAN REGION AMPHIPODA

Crustacea: Malacostraca: Amphipoda: Families and Genera

1	Urosoma dorsally vaulted, body not depressed; antenna II not massive, without teeth 2
1′	Urosoma dorsally flat, entire body slightly depressed; antenna I without accessory flagellum; antenna II several times thicker and twice longer than I, article 3 with some teeth ventroapically; gnathopod II without chela or subchela; Corophiidae 46
2(1)	Antenna I thinner, articles 2 and 3 longer 3
2′	Antenna I article 2 several times thicker than flagellum, articles 2 and 3 wider than long, 2 + 3 shorter than 1; telson entire Lysianassidae, one genus ..... *Pseudalibrotus*
3(2)	Gnathopods subchelate 4
3′	Gnathopods chelate ..... Caspicolidae, one genus ..... *Caspicola*
4(3)	Body carinate or knobbed 5
4′	Body not carinate 13
5(4)	Gnathopods not as below 6
5′	Gnathopods with article 6 attached to the strongly produced or extended apex of article 5; head with a long rostrum ..... Gammaracanthidae, one genus; *Gammaracanthus*
6(5)	Head with anteroventral tooth exceeding lateral cephalic lobe; Gammaridae (in part) 7
6′	Head with vestigial or no anteroventral tooth 8
7(6)	Telson broader than long; uropod III exopod lacking article 2 ..... *Axelboeckia*
7′	Telson as long as broad, uropod III exopod biarticulate ..... *Gmelinopsis*
8(6)	Pereopod VII, article 2 with large ventral lobe; antenna I accessory flagellum 2+ articles 9
8′	Pereopod VII, article 2 with minute lobe or smooth; antenna I accessory flagellum uniarticulate; Gammaridae (in part) 11
9(8)	Pereopod VI not much longer than pereopod VII; pereopod VII with articles 2–7 not particularly short; Gammaridae (in part) 10
9′	Pereopod VI much longer than pereopod VII, pereopod VII with articles 2–7 short ..... Pontoporeiidae, one genus; *Monoporeia*
10(9)	Uropod III not extended; urosomites spinose ..... *Amathillina*
10′	Uropod III strongly extended; urosomites with dorsomedian conical to cylindrical knobs ..... *Dikerogammarus*
11(8)	Dorsal carina single; lateral cephalic lobes quadrate, head lacking anterolateral wing ..... *Gmelina*
11′	Dorsal carina bilaterally double knobbed; lateral cephalic lobes protruding and rounded; head with anterolateral wing ..... *Kuzmelina*
13(4)	Maxilla I medial lobe with two or more setae in an apical or lateral row 14
13′	Maxilla I medial lobe with one or more setae in an apical bunch; maxilla II without facial oblique longitudinal setal row; uropod III exopodite article 2 well developed, endopodite scaliform; eyes absent ..... Niphargidae, one genus: *Niphargus*
14(13)	Maxilla I palp with articles subequal to each other; antenna II much shorter than antenna I; Behningiellidae 15
14′	Maxilla I palp with article 2 elongate or palp uniarticulate; antenna II not much shorter than antenna I 16
15(14)	Pereopods V–VII with article 2 not lobate; pereopod IV coxa weakly lobed ..... *Cardiophilus* (in part)
15′	Pereopods V–VII with article 2 lobate distoposteriorly ..... *Behningiella*
16(15)	Pereopod VII article 2 without posteriodistal lobe; Gammaridae (in part) 17
16′	Pereopod VII article 2 expanded and with a posteriodistal lobe 24
17(16)	Accessory flagellum uniarticulate; pereopod VII article 2 semicircular 18
17′	Accessory flagellum biarticulate 19
18(17)	Telson lamellate, deeply cleft; uropod III exopodite biarticulate and more than twice as long as sympodite ..... *Yogmelina* (in part)
18′	Telson thick, shallowly cleft; uropod III exopodite uniarticulate and less than twice as long as sympodite ..... *Scytaelina*
19(17)	Antenna II article 3 without ventral keel 20
19′	Antenna II article 3 with ventral keel ..... *Derzhavinella*
20(19)	Uropod III endopodite 50% of exopodite length or shorter 21
20′	Uropod III endopodite length 80% or more of exopodite length ..... *Gammarus*
21(20)	Antenna I article 3 longer than article 1 ..... *Sowinskya*
21′	Antenna I article 3 shorter than article 1 ..... *Echinogammarus* (in part)

22(21)	Uropod III marginal setae straight 23
22′	Male uropod III with marginal setae dense, long, and curled ..... *Trichogammarus*
23(22)	Uropod III marginal setae dense and longer than article width ..... *Echinogammarus* (in part)
23′	Uropod marginal setae only joined to spines and not longer than spines ..... *Chaetogammarus*
24(16)	Antenna I primary flagellum shorter than peduncle (usually shorter than article 1); accessory flagellum more than 40% length of primary flagellum; Pontogammaridae (in part) 25
24′	Antenna I primary flagellum longer than peduncle; accessory flagellum less than 40% length of primary flagellum 29
25(24)	Epimeron III face with posteroventral setal fan 26
25′	Epimeron III without setal fan 28
26(25)	Uropod III endopodite about one-third as long as exopodite 27
26′	Uropod III endopodite more than half as long as exopodite ..... *Uroniphargoides*
27(26)	Mandibular palp with D-setae; pereopod V article 2 unlobed ..... *Niphargoides*
27′	Mandibular palp without D-setae; pereopod V article 2 with posteriodistal lobe ..... *Compactogammarus*
28(25)	Mandibular palp lacking D-setae; uropod III exopodite article 2 elongate; antenna II articles 4 and 5 each about as long as article 3 (scarcely longer) ..... *Niphargogammarus*
28′	Mandibular palp with D-setae; uropod III exopodite article 2 not elongate, antenna II articles 4 and 5 significantly longer than article 3 ..... *Paraniphargoides*
29(24)	Gnathopod I stouter than gnathopod II 30
29′	Gnathopod I not stouter than gnathopod II 33
30(29)	Pereopods III–VII not prehensile; Gammaridae (in part) 31
30′	Pereopods III–VII prehensile ..... Iphigenellidae, one genus: *Iphigenella*
31(30)	Antenna I accessory flagellum 2+ articulate 32
31′	Antenna I accessory flagellum 1 articulate ..... *Yogmelina* (in part)
32(31)	Gnathopods strongly dissimilar, gnathopod II very thin; antennae elongate; epimeron III posterodistal corner with a short acute tooth ..... *Lanceogammarus*
32′	Gnathopods alike, gnathopod II scarcely smaller than gnathopod I; antennae short; epimeron III posterodistal corner with strong tooth ..... *Baku*
33(29)	Coxa IV with poorly developed posterior lobe; eyes situated at anterior margin of head 34
33′	Coxa IV with well-developed posterior lobe; eyes in middle of cephalic lobe 35
34(33)	Gnathopods large, gnathopod II enlarged; pereopod VII article 2 widely expanded and lobate ... Pontogammaridae (in part): *Pandorites*
34′	Gnathopods feeble, gnathopod II small but elongate; pereopod VII article 2 narrow and weakly lobate ..... Behningiellidae (in part): *Cardiophilus* (in part)
35(33)	Article 2 of pereopod VII with strong posterodistal lobe 36
35′	Article 2 of pereopod VII without posterodistal lobe 38
36(35)	Pereopods V–VII article 4 not dilated 37
36′	Pereopods V–VII article 4 dilated ..... Behningiellidae (in part): *Zernovia*
37(36)	Uropod III endopodite article 2 short, not marginally setose; coxae I–IV with short or no setae; antenna I of *Gammarus* form ..... Gammardiae (in part): *Shablogammarus*
37′	Uropod III endopodite article 2 elongate, with marginal setae; coxae I–IV with long setae; antenna I of *Pontogammarus* form ..... Pontogammaridae (in part): *Stenogammarus*
38(35)	Urosome with large knob(s) 39
38′	Urosome without knobs 41
39(38)	Head normal 40
39′	Head giant ..... Gammardiae (in part): *Cephalogammarus*
40(39)	Coxae I–IV and pereopods V–VII article 2 with strongly setose margins ..... Pontogammaridae (in part): *Turcogammarus*
40′	Coxae I–IV and pereopods V–VII article 2 with short and sparse setae ..... Gammaridae (in part): *Dikerogammarus*
41(38)	Pereopod IV article 4 with 10+ posterior setae (antenna I of *Pontogammarus* form) 42
41′	Pereopod IV article 4 with only 4–5 posterior setae (antenna I of *Dikerogammarus* form ..... Gammaridae (in part): *Akerogammarus*

42(41) Uropod III exopodite article 2 elongate, >15% length of article 1; antenna II first two flagellar articles together <95% as long as peduncle article 5 ..... Pontogammaridae (in part) 43

42′ Uropod III exopodite article 2 not elongate, <12 % length of article 1; antenna II first two flagellar articles together >80% as long as peduncle article 5 44

43(42) Uropod III exopodite article 1 with lateral plumose setae; pereopod II carpus trapezoidal, nearly as long as propodusus, in lakes along Volga River ..... *Stenogammarus* (*Wolgagammarus*)

43′ Uropod III exopodite article 1 without or very few lateral setae; pereopod II carpus triangular, much shorter than propodusus .... *Stenogammarus* (*Stenogammarus*)

44(42) Pereopod IV article 4 posterior setae in continuous fan 45

44′ Pereopod IV article 4 posterior setae divided into groups ..... Pontogammaridae (in part): *Obesogammarus*

45(44) Uropod III endopodite about half as long as exopodite ..... Cylindrostomidae, one genus: *Euxinia*

45′ Uropod III endopodite about one-third as long as exopodite ..... Pontogammaridae (in part): *Pontogammarus*

46(1) Antenna II, article 2 gland cone large, conspicuous; uropod III ramus short, broad, little longer than peduncle ..... *Corophium*

46′ Antenna II, article 2 gland cone small to medium, not prominent; uropods I and II rami with medial spines (setae); antenna II powerful, similar in both sexes, article 4 and flagellum short ..... *Chelicorophium*

LAKE BAIKAL REGION AMPHIPODA

Crustacea: Malacostraca: Amphipoda: Families and Genera

This key does not include questionable taxa. The position of genera in families follows Takhteev et al. (2015).

1 Antenna II peduncle article 5 not inflated distally, not much thicker than proximal flagellum articles 2

1′ Antenna II peduncle article 5 inflated distally, surrounded by a ring of plumose setae; flagellum articles much thinner than peduncle (Fig. 16.6.31 A, B) ..... Acanthogammaridae (in part); *Plesiogammarus*

2(1) Pleonite projections developed and provided with spines 3

2′ Pleonites with projections either absent or without spines 5

3(2) Dorsomedial row of elevations more or less developed; coxal plates II–IV inerm or with lateral spines, not on lower margins; Acanthogammaridae (in part) 4

3′ Dorsomedial row of elevations absent, dorsolateral rows as paired bulges; all pereonites and pleonites with spines; coxal plates II–IV with spine rows on lower margins; deep water species (Fig. 16.6.32) .... ?Pallaseidae (*incerta sedis*); *Polyacanthisca calceolata* Bazikalova, 1937

4(3) Body elongate; pereopods V–VII long, thin; eyes white, not visible in preserved specimens; antenna II flagellum flat, serrated on medial margin; large animals (Figs. 16.6.33 A, B) ..... *Garjajewia*

4′ Body compact, widened anteriorly; pereopods V–VII short, thick; eyes dark, always visible in preserved animals; antenna II flagellum not flattened nor serrated (Figs. 16.6.34 A, B) ..... *Brandtia*

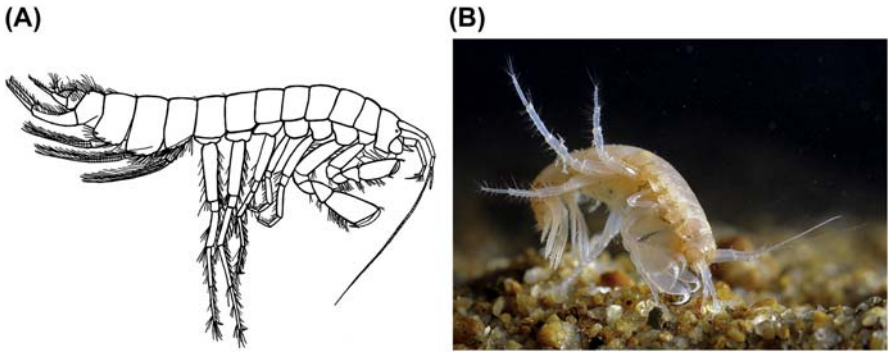


FIGURE 16.6.31 *Plesiogammarus brevis mazepowae*: (A) drawing by Vadim Takhteev, (B) photograph by Sergey Didorenko.

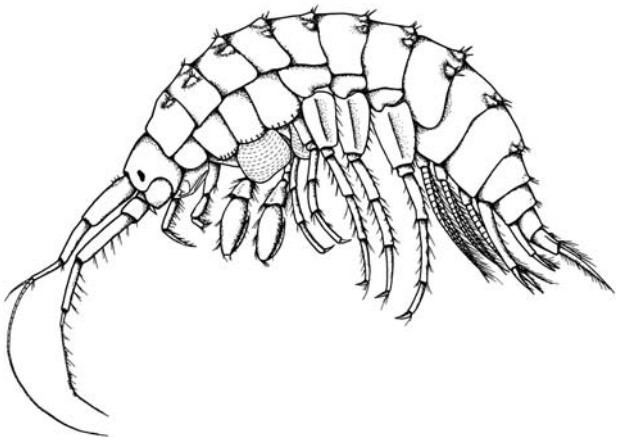


FIGURE 16.6.32 *Polyacanthisca calceolata*. Bazikalova, 1937 *Drawing by Irina Golenkova.*

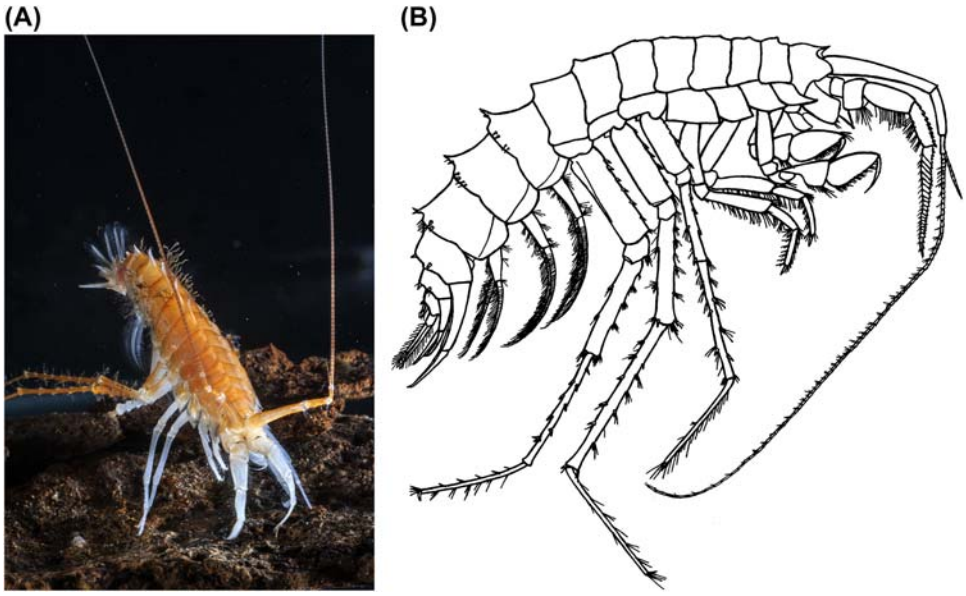


FIGURE 16.6.33 (A) *Garjajevia cabanisii cabanisii* (photograph by Sergey Didorenko); (B) *Garjajevia cabanisii pleshanovi. Drawing by Vadim Takhteev & Alexey Levashkevich.*

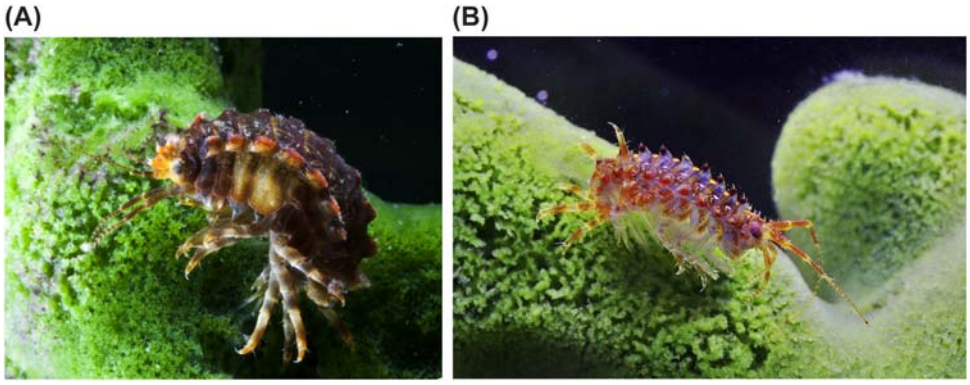


FIGURE 16.6.34 (A) *Brandtia (Brandtia) latissima lata*, (B) *Brandtia (Dorogostajskia) parasitica parasitica. Photograph by Sergey Didorenko.*

5(2) Dorsomedial row of elevations well developed at least on some segments, as spines, carinae (expanded and flattened distally, shaped like a button), or large, sharp tubercles 6

5′ Dorsomedial row of elevations absent or poorly developed as very low carinae or small bumps 11

6(5) Dorsomedial row of elevations is most developed on pereonites and pleonites, sometimes on urosomite I, but missing on II 7

6′ Dorsomedial row of elevations most developed on urosomites I and II ..... Acanthogammaridae (in part): *Coniurus*

7(6) Pleonite dorsolateral rows of protuberances in the form of weak tubercles or absent 8

7′ Pleonite dorsolateral rows of protuberances in the form of vertical spines (Fig. 16.6.35) ..... Acanthogammaridae (in part); *Propachygammarus*

8(7) Dorsomedial row of elevations keels or spiniform projections on first pereonites, increasing in size posteriorly 9

8′ Dorsomedial row of elevations most developed on pleonites II and III or only III (Figs. 16.6.36 A, B ..... Acanthogammaridae (in part); *Carinurus*

9(8) Dorsomedial row of elevations in the form of low carinae, blunt or pointed posteriorly 10

9′ Dorsomedial row of elevations in the form of sharp spines or blunt elevated carinae (Figs. 16.6.37 A, B) ..... Acanthogammaridae (in part); *Acanthogammarus*

10(9) Dorsomedial row of elevations in the form of low and blunt carinae (Fig. 16.6.38 A) ..... Acanthogammaridae (in part); *Hyalellopsis* (in part)

10′ Dorsomedial row of elevations in the form of long, tapered, flat carinae ..... Carinogammaridae (in part); *Carinogammarus* (in part)

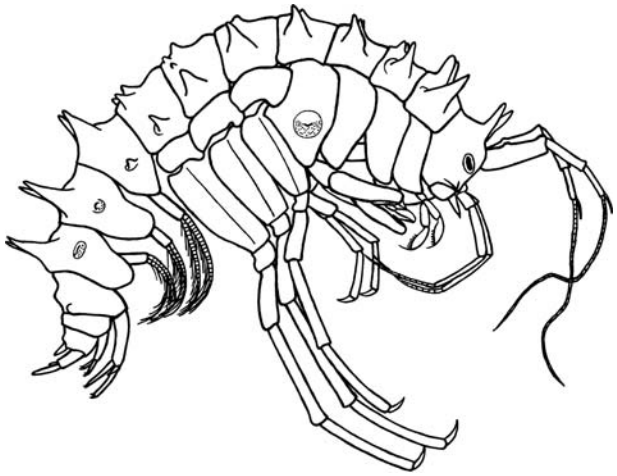


FIGURE 16.6.35 *Propachygammarus bicornis. Drawing by Vadim Takhteev.*

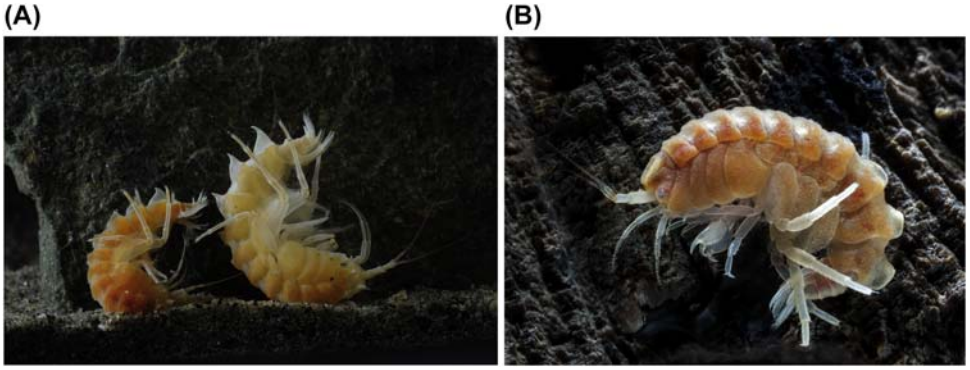


FIGURE 16.6.36 (A) *Carinurus reissnerii*; (B) *Carinurus platycarinus. Photographs by Sergey Didorenko.*

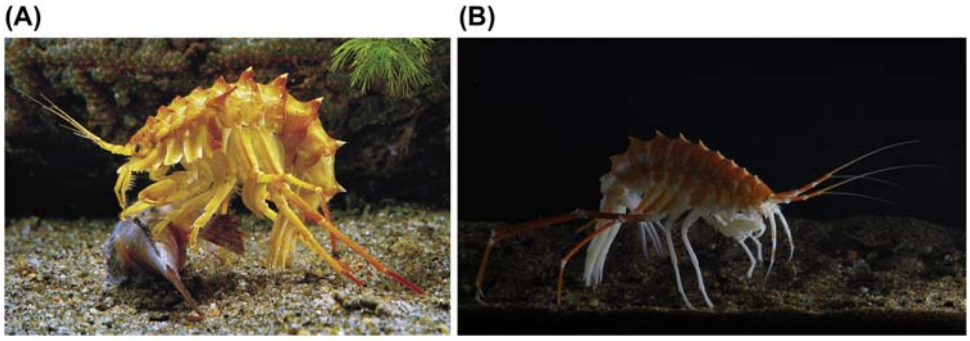


FIGURE 16.6.37 (A) *Acanthogammarus (Acanthogammarus) victorii*; (B) *Acanthogammarus (Brachyuropus) grewingkii*. *Photographs by Sergey Didorenko.*

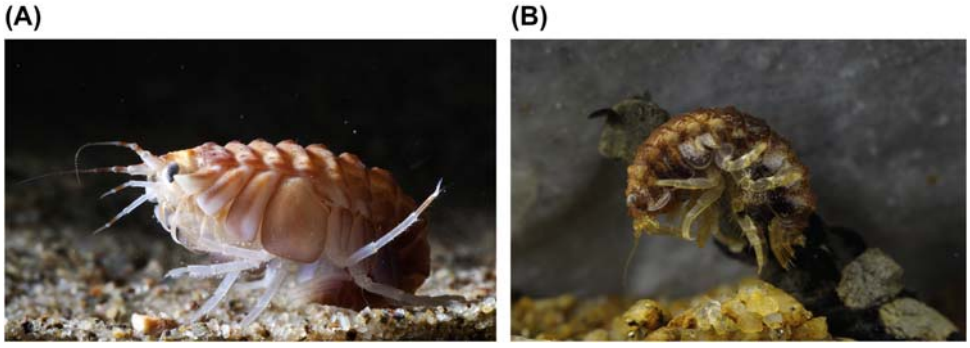


FIGURE 16.6.38 (A) *Hyalellopsis (Boeckaxelia) carpenterii carpenterii*; (B) *Hyalellopsis (Hyalellopsis)* sp. *Photographs by Sergey Didorenko.*



FIGURE 16.6.39 *Ceratogammarus cornutus. Photograph by Daria Bedulina, in the treatment by Sergey Didorenko.*

11(5)	Dorsomedial and/or dorsolateral rows of protuberances in the form of acute or blunt spiniform projection or well-developed carinae at least on some metameres	12
11′	Dorsolateral and/or marginal rows of protuberances absent or weak	16
12(11)	Body elongate, slender; uropod III normal or enlarged	13
12′	Body short and wide; uropod III short or rudimentary (Fig. 16.6.38 B)	Acanthogammaridae (in part); *Hyalellopsis* (in part)
13(12)	Anterior ventrolateral head corners rounded	14
13′	Anterior ventrolateral head corners extended into long, acute, spiniform projections (Fig. 16.6.39)	Pallaseidae (in part); *Ceratogammarus* (in part)

14(13)	Marginal rows of protuberances spiniform or carinate	15
14′	Marginal rows of protuberances low, rounded (Figs. 16.6.40 A, B)	Pallaseidae (in part): *Parapallasea*
15(14)	Uropod III with simple setae; pereopod dactyli (article 7) vestigial (Fig. 16.6.41)	Acanthogammaridae (in part); *Burchania meissneri* Bazikalova, 1935
15′	Uropod III with plumose setae; pereopod dactyli (article 7) normally developed (Figs. 16.6.42 A–C)	Pallaseidae (in part); *Pallasea*
16(11)	Median row of poorly defined protuberances in the form of low carinae or tubercles on at least some segments (in *Echiuropus levis* median tubercles may or may not be present)	17
16′	Median row of protuberances absent in all segments	25
17(16)	Body robust, wide	18
17′	Body slender or slightly widened anteriorly	20
18(17)	Antenna I accessory flagellum a single article	19
18′	Antenna I accessory flagellum of several articles	Acanthogammaridae (in part); *Cheirogammarus inflatus* (Sowinsky, 1915)
19(18)	Telson entire or only shallowly emarginate	Acanthogammaridae (in part); *Hyalellopsis* (in part)
19′	Telson cleft to base	Micruropodidae (in part); *Crypturopus* (in part)
20(17)	Uropod III exopodite of two articles	21

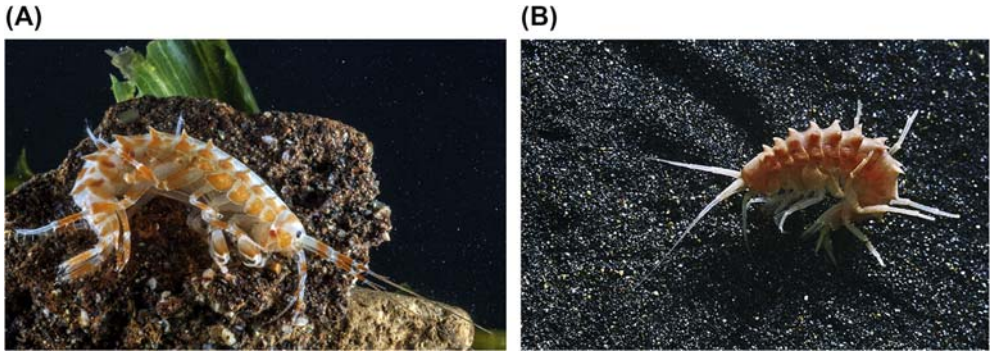


FIGURE 16.6.40 (A) *Parapallasea borowskii borowskii*; (B) *Parapallasea lagowskii*. *Photograph by Sergey Didorenko.*

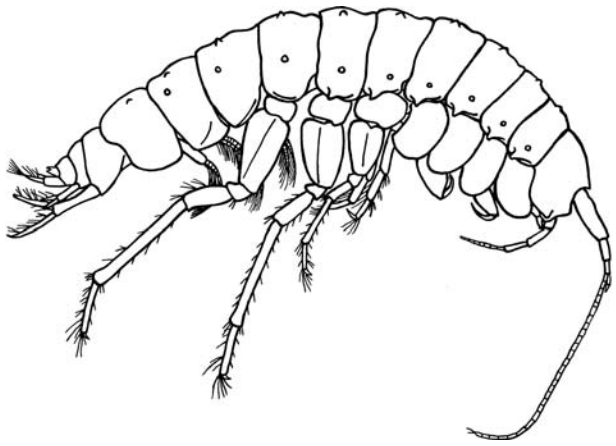


FIGURE 16.6.41 *Burchania meissneri*. *Drawing by Vadim Takhteev.*

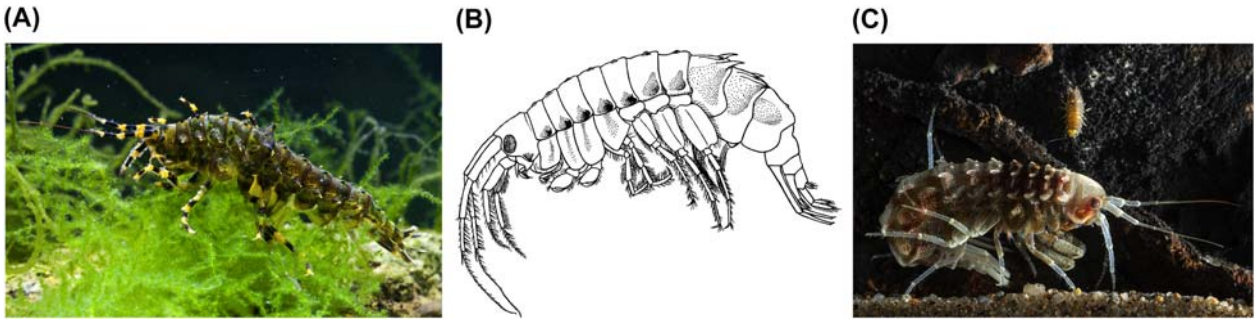


FIGURE 16.6.42 (A) *Pallasea (Pallasea) cancellus*; (B) *Pallasea (Pallasea) kesslerii*; (C) *Pallasea (Homalogammarus) brandtii*. *(A and C) Photographs by Sergey Didorenko; (B) drawing by Vadim Takhteev.*

20′	Uropod III exopodite of one article; Carinogammaridae (in part) 24
21(20)	Uropods I and II only with spines 22
21′	Uropods I and II armed with sparse spines and simple setae (Fig. 16.6.43) ..... Pallaseidae (in part); *Metapallasea*
22(21)	Uropods III exopod not more than twice the length of the endopod; exopod article 2 conical; Carinogammaridae (in part) 23
22′	Uropod III exopod not less than three times as long as the endopod; exopod article 2 very short (Fig. 16.6.44) ..... Micrurpodidae; *Gmelinoides*
23(22)	Pereopods VI and VII basipod (article 2) posterior margin with very short and sparse setae (Fig. 16.6.45) ..... *Carinogammarus* (in part)
23′	Pereopod VI and VII basipod (article 2) posterior margin, and often lateral surface with long or medium-length setae (Fig. 16.6.46) .... *Echiuropus* (in part)
24(20)	Mandibular palp distal article narrow, margins parallel, setal brush very short, shifted to distal end of the article ..... *Pseudomicruropus* (in part)
24′	Mandibular palp distal article lancet shaped ..... *Echiuropus* (in part)
25(16)	Antenna I proximally several times thicker than antenna II; antenna II with very long and thin articles 4 and 5; pereopods VI and VII long, very thin, filiform 26
25′	Antenna I proximal thickness subequal or less than antenna II 28
26(25)	Antenna I accessory flagellum with many articles; uropods I–III rami with plumose setae 27
26′	Antenna I accessory flagellum vestigial or absent; uropod I rami with small spines only, uropods II and III rami with dense plumose setae; males dwarf; pelagic (Fig. 16.6.47) ..... Macrohectopodidae; *Macrohectopus branickii* (Dybowsky, 1874)
27(26)	Excretory cone length equal to or shorter than antenna II article 3; most often on bacterial mats at lake bottom methane emissions ..... Pallaseidae (in part); *Leptostenus leptocerus* (Dybowsky, 1874)

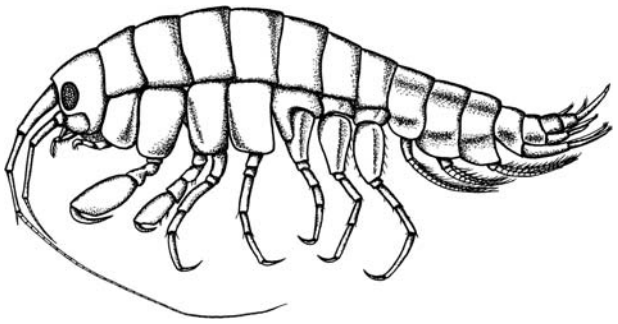


FIGURE 16.6.43 *Metapallasea galinae. Drawing by Irina Golenkova.*



FIGURE 16.6.44 *Gmelinoides fasciatus. Photograph by Sergey Didorenko.*



FIGURE 16.6.45 *Carinogammarus cinnamomeus. Photograph by Sergey Didorenko.*



FIGURE 16.6.46 *Echiuropus rhodophthalmus. Photograph by Sergey Didorenko.*

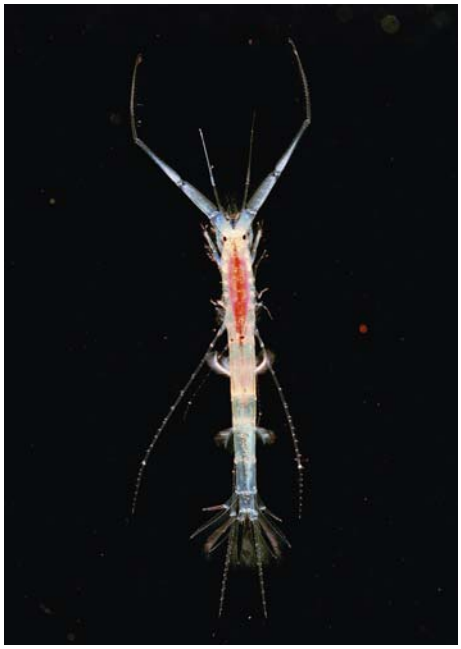


FIGURE 16.6.47 *Macrohectopus branickii*, female, from dorsal side. *Photograph by Sergey Didorenko.*

27′	Excretory cone obviously longer than antenna II article 3; nectobenthic, primarily below 200 m (Fig. 16.6.48) ..... Acanthogammaridae (in part); *Paragarjajewia*
28(25)	Antenna I and II subequal in proximal thickness; pereopods VI and VII with basipodite (article 2) posterior margin ranges from straight to a large lobe; pereopods VI and VII basipodites with distoposterior lobe absent to widely rounded or angular 29
28′	Antenna I proximally much thicker than antenna II; pereopods VI and VII with basipodite distoposterior margin never forming an extended angle or rounded lobe (Fig. 16.6.49) ..... Gammaridae (in part); *Corophiomorphus*
29(28)	Excretory cone directed anteriorly or distoanteriorly, variably long and thick 30
29′	Excretory cone long and thin, directed distoposteriorly toward the mouth; eyes very large, black, reniform; pereopods V–VII with basipodites bearing large, rounded distoposterior lobes; females much smaller than males (Fig. 16.6.50) ..... Micruropodidae; *Baikalogammarus pullus* (Dybowsky, 1874)
30(29)	Interantennal (genal) lobes protrude far beyond the short rostrum, sometimes turned into long spiniform growths; at least weak spines present on all pleonites 31
30′	Interantennal lobes not or only slightly longer than rostrum (if significantly longer, then spines on pleonite I absent) 32



FIGURE 16.6.48 *Paragarjajewia petersii. Photograph by Sergey Didorenko.*



FIGURE 16.6.49 *Corophiomorphus pachycerus. Photograph by Sergey Didorenko.*



FIGURE 16.6.50 *Baikalogammarus pullus*, male. *Photograph by Sergey Didorenko.*

31(30)	Pereonites V–VII and posterior segments with spines; uropod II with spines only ..... Pallaseidae (in part); *Ceratogammarus* (in part)
31′	Pleonite I and posterior segments with spines; uropod II endopodite with simple short setae and spines; found at great depths .... Gammaridae (in part); *Lobogammarus latus* Bazikalova, 1945
32(30)	Uropod III always with plumose setae (at least one, usually many), uropods I and II also sometimes with plumose setae 33
32′	Uropod III typically without plumose setae, uropods I and II always without plumose setae, or if a few plumose setae among simple setae, then uropod III exopod of two articles, pereopods V–VII with basipodite posterior margin without long setae, and the antenna I accessory flagellum of many articles 44
33(32)	Pereonite margins and interantennal lobes do not form triangular processes 34

33′ Pereonite margins extend ventrolaterally as triangular extensions, covering the upper part of the coxal plates; head strongly convex, with rostrum bent ventrally; interantennal lobes projecting as ventrally directed triangular processes; regularly on algae ..... Pallaseidae (in part); *Hakonboeckia strauchii* (Dybowsky, 1874)

34(33) Antenna I accessory flagellum of not less than two normally developed articles 35

34′ Antenna I accessory flagellum of 1–2 articles, if two articles, then article 2 greatly reduced, barely noticeable ..... Micruropodidae (in part); *Micruropus* (in part)

35(34) Uropod III rami subequal, exopod only one article, or two articles then uropods I and II densely covered with simple setae; uropod III rami with marginal plumose setae; rostrum may be long and acute; Pallaseidae (in part) 36

35′ Uropod III exopod obviously longer than endopod, of two articles, or if only one article, it is several times longer than endopod; uropod III exopod lateral margin sometimes without plumose setae; rostrum short, blunt, or absent; Gammaridae (in part) 37

36(35) Uropod III rami laterally with plumose setae, distally with a cluster of simple setae (Figs. 16.6.51 A, B) ..... *Poekilogammarus*

36′ Uropod III rami laterally with plumose setae, distally with three spines, simple setae absent ..... *Gymnogammarus*

37(35) Spines present on urosomites; pleonites smooth or posterior margins with single, very short setae 38

37′ At least posterior four metameres with spines (if spines only urosomites, then pleonite III posterior margin and often also dorsal surface with obvious, long setae) 42

38(37) Pereopods V–VII basipodites (article 2) with posterior margins distally tapering off or angular 39

38′ Pereopods V–VII basipodites (article 2) with posterior margins acute, spiniform projections (Figs. 16.6.52 A, B) ..... *Odontogammarus*

39(38) Eyes small, narrow, oval or reniform, their length less than or only slightly larger than the diameter of antenna I proximal article 40

39′ Eyes large, broadly reniform or irregular, with incised edges, eye height obviously greater than the diameter of the antenna I proximal article (Fig. 16.6.53) ..... *Ommatogammarus*

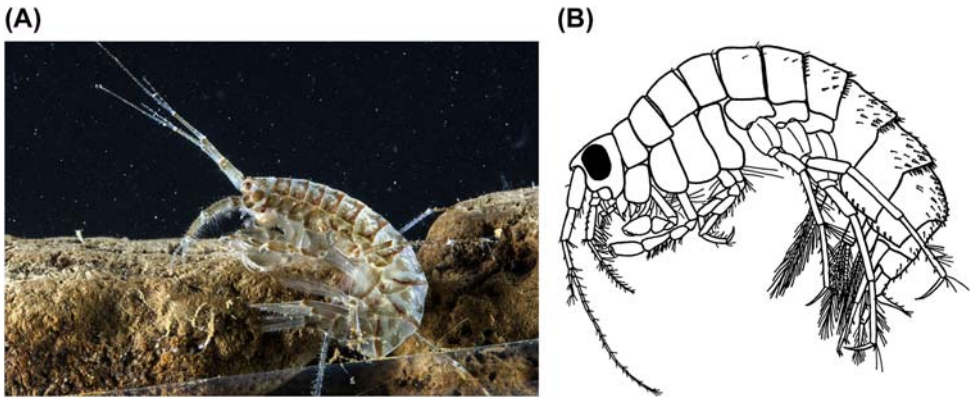


FIGURE 16.6.51 (A) *Poekilogammarus (Poekilogammarus) sukaczewi* ; (B) *Poekilogammarus (Onychogammarus) araneolus. (A) photograph by Sergey Didorenko, (B) Drawing by Vadim Takhteev.*

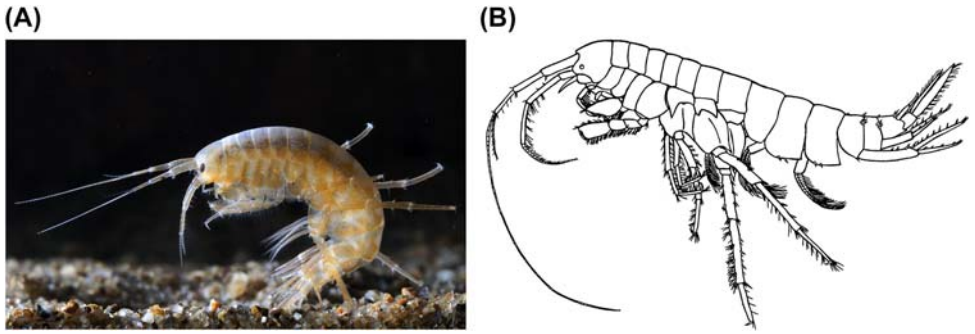


FIGURE 16.6.52 (A) *Odontogammarus calcaratus*; (B) *Odontogammarus bekmanae. (A) Photograph by Sergey Didorenko; (B) drawing by Vadim Takhteev.*



FIGURE 16.6.53 *Ommatogammarus albinus. Photograph by Sergey Didorenko.*



FIGURE 16.6.54 *Heterogammarus sophianosii. Photograph by Sergey Didorenko.*

40(39)	Pereopod VII basipodite posteriodistal margin projecting as a distinct angle 41
40′	Pereopod VII basipodite posteriodistal margin not well developed (Fig. 16.6.54) ..... *Heterogammarus* (in part)
41(40)	Lives only in open, cold water Baikal (Figs. 16.6.55 A, B) ..... *Eulimnogammarus* (in part)
41′	Limited to shallow warmed bays ..... *Gammarus lacustris* Sars, 1863
42(37)	Maxilliped palp dactylus normally long; eyes reniform or oval 43
42′	Maxilliped dactylus palp rudimentary; eyes large, irregularly shaped, lower portion greatly expanded; large deep-water animals ..... *Abyssogammarus* (in part)
43(42)	Antenna II article 3 with a distolateral outgrowth, ending in a cluster of long setae; article 4 expanded distally and more than twice as thick as article 5 proximal end ..... *Abyssogammarus* (in part)
43′	Antenna II not as above ..... *Eulimnogammarus* (in part)
44(32)	Mandibular palp dactylus widened medially, setal brush developed, if setal brush absent, then dorsal margin with dense setal tufts 45
44′	Mandibular palp dactylus long and narrow with only apical setae, setal brush absent or very short and shifted to apex; body up to 5 mm with rounded dark eyes ..... Carinogammaridae (in part); *Pseudomicruropus* (in part)
45(44)	Body short, wide; pereopods short 46
45′	Body elongate, cylindrical, or only slightly expanded anteriorly 49
46(45)	Antenna I accessory flagellum a single article 47
46′	Antenna I accessory flagellum with at least two articles; parasites in marsupium of large, mostly deep water amphipods feeding on eggs (Fig. 16.6.56) ..... Pachyschesidae; *Pachyschesis*
47(46)	Telson cleft to base; uropod III often short, but not rudimentary; Micruropodidae (in part) 48
47′	Telson entire; uropod III rudimentary ..... Acanthogammaridae (in part); *Hyalellopsis* (in part)

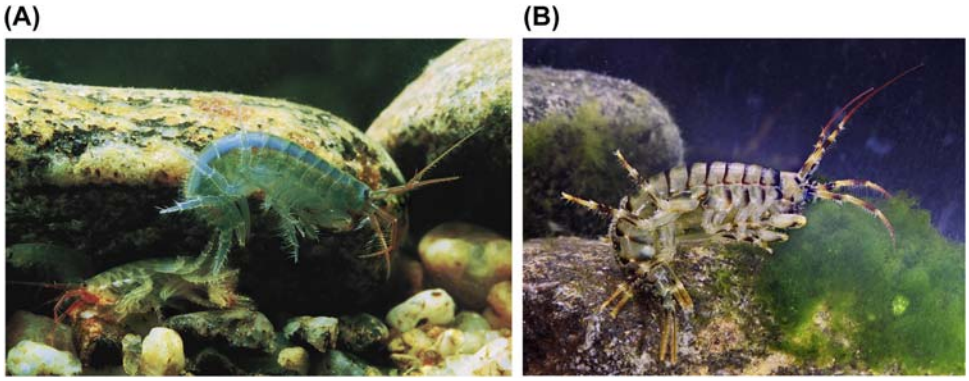


FIGURE 16.6.55 (A) *Eulimnogammarus cyaneus*; (B) *Eulimnogammarus verrucosus. Photograph by Sergey Didorenko.*

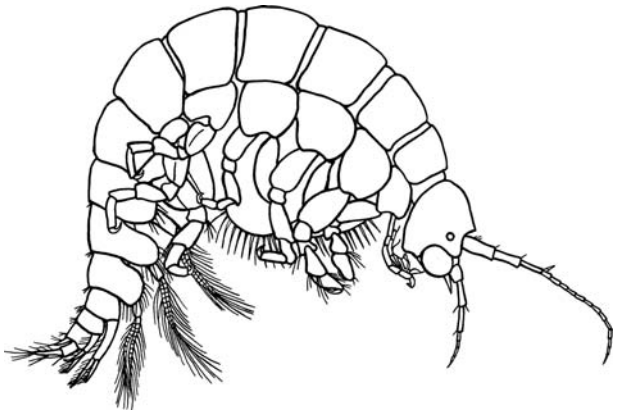


FIGURE 16.6.56 *Pachyschesis bazikalovae*, female. *Drawing by Vadim Takhteev.*



FIGURE 16.6.57 *Crypturopus inflatus. Photograph by Sergey Didorenko.*

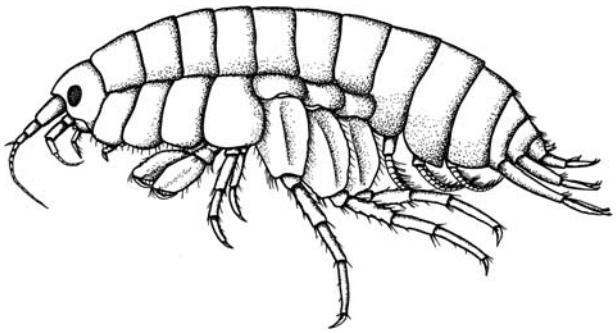


FIGURE 16.6.58 *Micruropus galasii. Drawing by Irina Golenkova.*



FIGURE 16.6.59 *Macropereiopus* sp. *Photograph by Sergey Didorenko.*

48(47)	Eyes in preserved specimens visible, widely separated on a wide and low head, facing dorsolaterally; adult body length greater than 6 mm (Fig. 16.6.57) ..... *Crypturopus*
48′	Eyes in preserved specimens not visible; adult body length 4–6 mm ..... *Homocerisca*
49(45)	Pereopods V–VII with basipodite posterior margin bearing small spines or very short single setae 50
49′	Pereopods V–VII with basipodite posterior margin bearing rather long (and often dense) setae 52
50(49)	Pereopods V–VII with basipodite projecting posteriodistal angle forming a rounded lobe; body less than 10 mm 51
50′	Pereopods V–VII with basipodite projecting posteriodistal margin tapering distally or with a distinct angle or if rounded, then accessory flagellum of 5–10 articles; length between 4 and 40 mm; Gammaridae (in part) ..... *Eulimnogammarus* (in part)
51(50)	Urosomites with spines; antenna I accessory flagellum of 1–2 articles; uropod III exopod with two articles, distal article obviously conical; Gammaridae (in part) ..... *Bazikalovia*
51′	Urosomites with small setae; antenna I accessory flagellum of 3–4 articles; uropod III very short, exopod of one article; ?Micruropodidae (in part) ..... *Profundalia*
52(49)	Accessory flagellum with at least two normally developed articles; eyes of live animals white, small, not visible in preserved specimens 53
52′	Accessory flagellum with one article, rarely with a very short article 2; eye typically dark (Fig. 16.6.58) ..... Micruropodidae (in part); *Micruropus* (in part)
53(52)	Pereopods V–VII with basipodite cylindrical, posterior margin not developed or proximally rudimentary ..... Acanthogammaridae (in part); *Koshovia*
53′	Pereopods V–VII with basipodite wide or narrow, but always with posterior margin clearly defined and projecting (Fig. 16.6.59) ..... Gammaridae (in part); *Macropereiopus*

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Malacostraca: Tanaidacea

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INTRODUCTION

Tanaidaceans are predominately benthic marine and estuarine inhabitants of tidal influenced rivers, bays, salt marshes, beaches, and near shore and offshore marine environments. Although over 1000 species are known, few are found in oligohaline conditions (0.5–5 ppt), and most species reported from fresh water (<0.5 ppt), may only be exposed temporarily to this condition.

Palaearctic freshwater tolerance in tanaidacea is limited to the families Leptocheliidae and Tanaidae in the suborder Tanaidomorpha. These tanaidaceans are all domicolous and water contained in the tube, as well as interstitial water trapped in sediment, may allow them to survive seasonal and tidal variations in salinity of the external water (R. Heard personal communication).

LIMITATIONS

A population of a single species will usually contain mancas (= postlarval juveniles), neuters, and adult males and females. An adult male or female may be needed to confirm a determination. Some tanaidomorph tanaidaceans have a very small terminal article to the first antenna that may not be apparent at lower magnification and is not counted in the key.

There are likely unrecorded Palaearctic taxa that should be included in future keys. Several studies have examined the global distribution of freshwater tanaids including Jaume & Boxshall (2008) and Balian et al. (2008). Within the Palaearctic, there remains an enigmatic record of *Paraleptognathia longiremis* from Lake Baikal, but its accuracy is doubtful (Guerrero-Komritz, 2004, personal communication; Jaume & Boxshall, 2008). *Tanaissus liljeborgii*, although reported from European beaches near a freshwater stream (Bird, 2002), is not considered a freshwater tolerant species and is not included here. Other Palaearctic taxa have wide global distributions in euryhaline environments, such as *Sinelobus stanfordi* (Richardson, 1901) (see Gardiner, 1975; Sieg, 1981; Haaren & Soors, 2009).

TERMINOLOGY AND MORPHOLOGY

Dojiri and Sieg (1997) provide a detailed account of external morphology. Tanaidaceans are most easily recognized by their small size (1–75 mm); adults have six pairs of **pereopods**, and the first ambulatory thoracic appendages are chelate. The body is usually dorsoventrally flattened or subcylindrical, consisting of a **cephalothorax** with sessile eyes, six **pereonites**, five **pleonites,** and a **pleotelson**. The **uropods** are terminal, a characteristic shared with some isopods.

Tanaidaceans, as in other Peracarida, brood their young in a brood pouch originating from coxal outgrowths of the pereopods. The young are manca and resemble adults except that they lack the sixth pereopod. Sexual dimorphism is strong in some species, with adult males bearing large chelae and a laterally compressed cephalothorax, as in, for example, *Heterotanais oerstedii* Kroyer, 1842. Functional mouthparts are absent in the Tanaidomorpha (e.g., *Leptochelia* spp.)

MATERIAL PREPARATION AND PRESERVATION

Tanaidaceans can be collected by hand, cores, or various types of grabs. Sediments containing tanaidaceans can be preserved in situ, or tanaids can be extracted by repeated water washings and elutriation. The latter is usually done with a bucket by swirling and decanting of the invertebrates in the sediment samples. Collected material preserved in situ is washed with gentle pressure through a graded series of sieves, and specimens are usually retained on a 500 μm sieve. Tanaidaceans are usually preserved in 10% formaldehyde and stored in 70% ethanol.

Because of their small size, tanaidaceans must be examined with a dissecting microscope, and often individual appendages, especially mouth parts, must be removed, mounted, and examined with a compound microscope. Dissection is usually done in ethanol with fine forceps or chemically sharpened tungsten needles (Larsen, 2005). Temporary mounts can be prepared with glycerin alcohol on slides with coverslips.

KEYS TO TANAIDACEA

Tanaidacea: Tanaidomorpha: Families

1 Uropod uniramus (no exopod present); abdomen with four unfused pleonites; pleonites I and II each with an obvious transverse row of long plumose seta ..... **Tanaidae [p. 856]**

1′ Uropod biramous (exopod present) with endopod having three or more articles ..... **Leptocheliidae [p. 856]**

Tanaidacea: Tanaidomorpha: Tanaidae: Genera and Species

1 Adult uropod with three articles total; article 2 distinctly longer than 1 and 3 ..... *Tanais dulongii* (Audouin, 1826)

1′ Adult uropod with four articles total; article 2 not distinctly longer than other articles ..... *Sinelobus stanfordi* (Richardson, 1901)

Tanaidacea: Tanaidomorpha: Leptocheliidae: Genera and Species

1 Female second antenna article 2 lacking thorn setae, article 3 lacking a dorsodistal process; male first antenna flagellum with three or fewer articles bearing aesthetasc; male chela with pollex clavate, distally expanded with apex blunt, flattened, extending obliquely backward from propodus proximal margin ..... *Heterotanais oerstedii* (Kroyer, 1842)

1′ Female second antenna article 2 with thorn setae, article 3 bearing a dorsodistal process; male first antenna flagellum seven or more articles bearing aethetascs; male chela with pollex not clavate ..... *Leptochelia savignyi* (Kroyer, 1842)

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Malacostraca: Isopoda

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INTRODUCTION

Palaearctic freshwater isopods are typically inhabitants of streams of all sizes, temporary pools, ponds, lakes, and rivers where they may be found on the substrate, under stones and other debris, or at times crawling about vegetation. Perhaps over half of the described species are obligatory inhabitants of groundwater, where they are found in caves or other habitats where subterranean waters flow through unconsolidated deposits (e.g., gravel, sand, soil). Some stenasellids inhabit thermal waters.

LIMITATIONS

The world list of isopods, maintained by WoRMS (http://www.marinespecies.org/isopoda), reports 235 described Palaearctic taxa in the Asellidae and 63 taxa in the Stenasellidae. It is difficult to gauge the numbers in other families, as there are many known undescribed species. Thus, most of the keys stop at genus level. Several genera are badly in need of revision, and many taxa undoubtedly remain to be discovered given the propensity of these crustaceans to inhabit groundwater habitats.

The two Palaearctic aselloid families can be identified without dissection and using low power magnification. Beyond that it is generally necessary for careful specimen preparation and dissection under high magnification. Range and habitat information are helpful. Endemicity is pronounced and some taxa can be identified based on collection location and ecological data. Some genera are dubious, and different workers have treated them in various classification permutations. Definitive answers will have to await a thorough morphological and genetic comparison of the groups. Many species undoubtedly remain to be described.

The stenasellids are restricted to subterranean habitats including thermal waters. As a group these isopods are rare, difficult to find and undoubtedly more remain to be discovered. Like the asellids, identification is largely restricted to male characters. That fact wreaks havoc with identification since two monotypic genera *Johannella* (from a thermal spring in Algeria) and *Acanthastenasellus* (from Somalia) are known only from females. The stenasellids most likely to be encountered north of Africa belong to the genera *Stenasellus* and *Magniezia*, which contains 42 species across the Palaearctic and undescribed species continue to be found. Endemic to the Balkans are the genera *Balkanostenasellus* (two species) and *Protelsonia* (four species). The species of these genera are generally allopatric and identification is aided by geography.

The stenasellid genera *Metastenasellus* (seven species) and *Magniezia* (five species) are endemic to Africa where they occur with *Stenasellus*. These three genera are separated from one another by the form of the male second pleopodal endopod. In *Metastenasellus* the endopod is functionally unarticulate, and torsion is obvious. In *Magniezia* and *Stenasellus* the endopod is obviously biarticulate and bent midlength, with elongation and slight torsion in *Stenasellus*, but short and lacking torsion in *Magniezia*. The remaining monotypic genus endemic to Africa is *Parastenasellus* (*P. chappuisi* from Ivory Coast), which can be distinguished by its greatly reduced male pleopod 2 exopod.

TERMINOLOGY AND MORPHOLOGY

The smallest of the Aselloidea are <2 mm long, although most are somewhat longer. Epigean species are frequently mottled brown in appearance, with their unpigmented subterranean counterparts a whitish color. Likewise, eyes are present in the surface species and vary from being reduced to completely absent in subterranean species. The body is comprised of three main sections (Fig. 16.6.60 A). The head contains the two pairs of antennae and the mouthparts, called (in sequence) the **mandibles** (sometimes with palps), two pairs of **maxillae**, and the **maxillipeds**. The thorax is comprised of seven **pereonites**, each with a pair of **pereopods**. The first pereopod pair may be modified for grasping with the penultimate article (the **propodus**) enlarged and opposed by the final article (the **dactylus**). The abdomen is comprised of five somites known as **pleonites**, with appendages called **pleopods**. The pleonites in some groups are fused into a **pleotelson**. In the predominant asellids the second pleopod of the male is modified as a sperm reservoir and transfer mechanism. The apex of the male second pleopod endopod possesses a sperm transfer tube, called the **cannula**, which has a unique construction in each species, and is frequently surrounded by accessory processes. The identification of most asellid species relies on the examination of this structure. The terminal appendages are the uropods, which vary in their form and place of attachment to the pleon.

MATERIAL PREPARATION AND PRESERVATION

Isopods should be placed in 70% ethyl alcohol; however, 80%–95% may be required if many specimens are taken, thereby preventing dilution from the animal's high body water content. Specimens are best examined in 70% ethanol and viewed under low power magnification for family, or sometimes, genus level determination. Species identification frequently requires dissection of at least the male second pleopod, which can be accomplished by manipulating the specimen with fine forceps and probes constructed of insect minuten pins (minuten nadeln). By repeatedly piercing the exoskeleton in the sutures between the ventral pleonites, the tiny second pleopod can be teased away from the specimen.

The simplest procedure is to transfer the appendage into a drop of glycerin on a microscope slide. It is usually a good idea to look at the positioning of the pleopod in the glycerin to ensure than nothing needs to be adjusted before placing the coverslip. The pleopod is now ready for examination, which depending on the size of the specimen, may require 400–1000x for evaluation of the tip

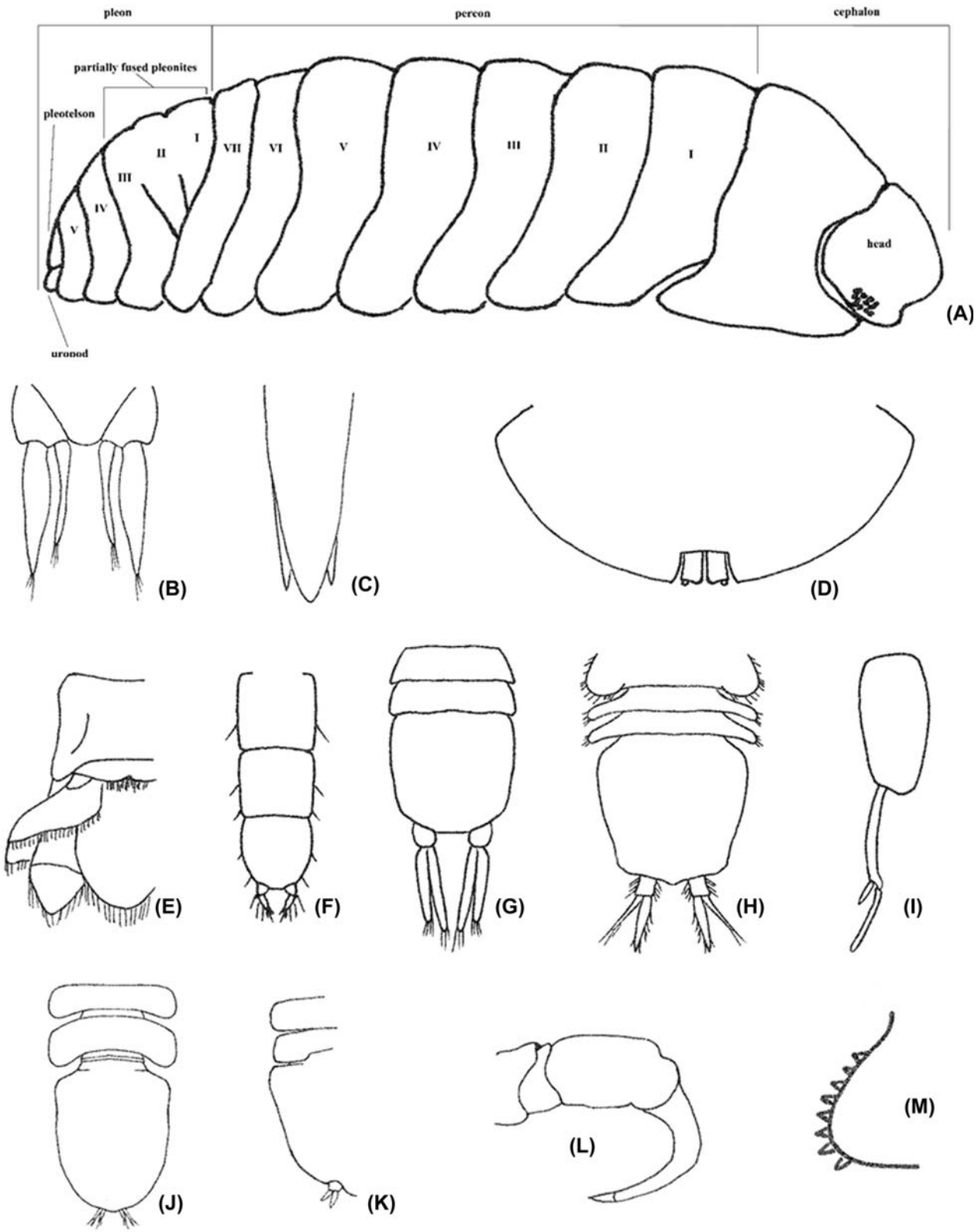


FIGURE 16.6.60 Inland water isopods: (A) generalized view of an isopod, left lateral view; (B) *Cantabroniscus primitivus*, telson and uropods; (C) *Saduria entomon*, telson and uropods; (D) *Jaera* sp., telson and uropods; (E) *Cyathura* sp., left half telson and uropod; (F) *Microparasellus* sp., telson and uropods; (G) Stenasellidae, telson and uropods; (H) Stenasellidae, telson and uropods; (I) *Phreatoasellus*, left half telson and uropod; (J) *Uénasellus iyoensis*, telson and uropods; (K) *Nipponasellus* sp., left half telson and uropod; (L) Cymothidae, pereopod III articles (left to right): merus (incomplete), carpus, propodus, dactylus; (M) *Microparasellus* sp., pereonite VI, left half.

structures of the male second pleopod endopod. After examination the pleopods should be removed from the slide and placed in a microvial within the vial that accompanies the dissected specimen.

ACKNOWLEDGMENTS

We are especially grateful to Niel Bruce and George (Buz) Wilson. Dr. Bruce proofread an earlier version of this text, and both Drs. Bruce and Wilson supplied some important references.

KEYS TO ISOPODA

The Palaearctic freshwater Isopoda are very poorly known, and we strongly suspect that only a fraction of the actual isopod diversity has been described. Wilson (2008) estimated that worldwide freshwater isopod diversity was only about 37% described. Therefore, we strongly suggest that users of these keys be careful not to force a given specimen into one of the taxa presented. Rather, we encourage the user to use this key as a starting point, to direct the user to the original literature to make a proper determination.

Malacostraca: Isopoda: Suborders

1	Uropods styliform, inserted terminally on pleotelson; body length variable (Figs. 16.6.60 B, D, F–K) 2
1′	Uropods lamellar, inserted at pleotelson base; body length <4x width (Figs. 16.6.60 A, C, E) 4
2(1)	One, two, or three free pleonites; body length variable 3
2′	Free pleonites; uropods; body length less than five times width; pigment and eyes absent ..... (Fig. 16.5.60 B) ..... Oniscidea, one species *Cantabroniscus primitivus* Vanel, 1965 [Spain]
3(2)	Two long pleonites, and a pleotelson, all cylindrical; body length at least six times width; subterranean ..... Microcerberidea, Microcerberidae, one genus: *Microcerberus* [Mediterranean Region, North Africa. Probably many undescribed species]
3′	One or two, free pleonites; body length variable ..... **Asellota [p. 859]**
4(1)	Uropods not modified as a ventral operculum (Fig. 16.6.4) 5
4′	Uropods modified as opercula, covering pleopods (Figs. 16.6.3 and 60 C) .... Valvifera, one species: *Saduria entomon* (Linnaeus, 1758) [Northern Europe, Russia (Siberia), Caspian Sea, Black Sea. Nearctic]
5(4)	Uropods articulating mediolaterally; pleon dorsally with four or five free pleonites plus the pleotelson (Fig. 16.6.60 E) ..... **Cymothoida [p. 860]**
5′	Uropods, particularly the peduncle/protopod, articulating dorsoventrally; pleon dorsally with four or fewer free pleonites plus the pleotelson ..... Sphaeromatidea, one family: **Sphaeromatidae [p. 862]**

Malacostraca: Isopoda: Asellota: Families

1	One or zero free pleonites visible dorsally 2
1′	Two free pleonites 4
2(1)	Pleotelson lateral margins parallel; body elongate, length at least six times body width 3
2′	Pleotelson posterolateral margins converging; uropods shorter than pleotelson; body broad in dorsal view, length less than four times width (Fig. 16.6.60 D) ..... **Janiridae [p. 859]**
3(2)	Uropods biramous ..... Lepidocharontidae, one genus; *Microcharon* [Europe, peri-Mediterranean, Central Asia. Oriental, Neotropical]
3′	Uropods uniramous (Fig. 16.6.60 F) ..... **Microparasellidae [p. 859]**
4(1)	Antenna II without an exopod; pleonites I and II regressed, short and narrow, not pronounced in dorsal view (Figs. 16.6.60 I–K) ..... **Asellidae [p. 859]**
4′	Antenna II with an exopod; pleonites I and II wide, not regressed pronounced in dorsal view (Figs. 16.6.60 G, H) ..... Stenasellidae [Widespread Palaearctic. Ethiopian Region. In need of revision, genera unclear]

Malacostraca: Isopoda: Asellota: Janiridae: Genera

1	Pleotelson rhomboidal; body broad in dorsal view, length <4x width (Fig. 16.6.60 D) ..... *Jaera* [Europe]
1′	Pleotelson oval; body elongate in dorsal view, length ~6x width ..... *Mackinia* [Japan, Korea, Russia]

Malacostraca: Isopoda: Asellota: Microparasellidae: Genera

1 Somite lateral margins smooth ..... *Angeliera phreaticola* Chappuis & Delamare-Deboutteville, 1952 [France, Italy]

1′ Somite lateral margins edged with denticles (Fig. 16.6.60 M) ..... *Microparasellus* [Lebanon, Macedonia]

Malacostraca: Isopoda: Asellota: Asellidae: Genera

Only males can be identified with this key.

1 Coxae not obscured by pereonites, visible in dorsal view 2

1′ Coxae obscured by pereonites, not visible in dorsal view ..... *Bragasellus* [Portugal, Spain]

2(1) Both pleopod I protopodites at least partially fused at base 3

2′ Pleopod I protopodites not fused at base 6

3(2) Head not elongate 4

3′ Head elongate, twice as long as wide ..... *Psammasellus capitatus* Braga, 1968 [Portugal]

4(3) Mandibular palp present 5

4′ Mandibular palp absent ..... *Synasellus* [Portugal, Spain]

5(4) Pleopod II with complex tip processes ..... *Chthonasellus bodoni* Argano & Messana, 1991 [Italy]

5′ Pleopod II endopod without accessory apical processes ..... *Stygasellus phreaticus* (Chappuis, 1943) [Romania]

6(2) Pleopod II endopodite lacking basal spur 7

6′ Pleopod II endopod with basal spur 9

7(6) Pleopod II endopod without pronounced basal apophysis 8

7′ Pleopod II endopod with pronounced basal apophysis ..... *Gallasellus heilyi* (Legrande, 1956) [France]

8(7) Pleopod II endopod distally tapering to a point ..... *Baicalaselllus* [Lake Baikal]

8′ Pleopod II endopod distally not tapering to a point ..... *Proaselllus* [Western Palaearctic]

9(7) Pleopod II endopod bulbous distally 10

9′ Pleopod II endopod tapering distally (Fig. 16.6.60 K) ..... *Nipponasellus* [Japan]

10(9) Uropods inserted distally 11

10′ Uropods inserted ventrally (Fig. 16.6.60 J) ..... *Uénasellus iyoensis* Matsumoto, 1960 [Japan]

11(10) Pleotelson length and width subequal; uropod peduncle subequal to or shorter than pleotelson, uropod exopod length ≥0.5x endopod 12

11′ Pleotelson longer than wide; uropod peduncle and endopod each longer than pleotelson, uropod exopod length ~0.25x endopod (Fig. 16.6.60 I) ..... *Phreatoasellus* [Japan]

12(11) Dorsum with setation reduced, covered with squamellae ..... *Sibirasellus parpurae* Henry & Magniez, 1993 [Siberia]

12′ Dorsum with setation normal, not covered with squamellae ..... *Asellus* [Palaearctic. Nearctic]

Malacostraca: Isopoda: Cymothoida: Superfamilies

1 Bilaterally symmetrical; adults not obligate, sessile parasites on crustaceans or fish 2

1′ Females bilaterally asymmetrical; males symbionts living on female's body; obligatory parasites of crustaceans (Figs. 16.6.60 C and 61) ..... Bopyroidea

2(1)	Uropod exopod curving over pleotelson dorsum; maxilliped coxae fused to head; body elongate, length at least five times width (Figs. 16.6.5 and 60 E) ..... Anthuridea, one genus: ***Cyathura*** **[p. 860]**
2′	Uropod exopod not curving over pleotelson dorsum; maxilliped coxae freely articulate; body length four times width or less ..... **Cymothooidea [p. 861]**

Malacostraca: Isopoda: Cymothoida: *Cyathura*: Species

This genus has numerous marine and brackish water species, however, only three are truly freshwater in the Palaearctic.

1	Male pleopod II lateral margin without spines, apex margined with 20+ plumose setae 2
1′	Male pleopod II lateral margin bearing spines, apex with less than 10 plumose setae ..... *Cyathura wadinicola* Botosaneanu & Stock, 1997 [Oman]
2(1)	Male pleopod II, with appendix masculina apically bifurcate ..... *Cyathura shanghaiensis* Liu, Poore, & Chen, 2013 [China]
2′	Male pleopod II, with appendix masculina apically simple ..... *Cyathura furcata* Nunomura & Hagino, 2000 [Japan]

Malacostraca: Isopoda: Cymothoida: Cymothooidea: Genera

1	Dactyls strongly recurved, hamulate; antennae with peduncle and flagellum distinctly different; maxilliped palp with two or more palpomeres 2
1′	Dactyls longer than propodi; antennae with peduncle and flagellum not distinctly different; maxilliped palp with only two palpomeres (Fig. 16.6.60 L) ..... Cymothidae [Widespread]
2(1)	All or no pereopods with dactyls recurved, hamulate; maxillae not styliform; maxillipeds lacking stout, arcuate setae 3
2′	Pereopods I–III with at least some dactyls recurved, hamulate; maxillae styliform, elongate; maxillae I, II, and maxillipeds apically with stout, arcuate setae ..... Aegidae
3(2)	Pereopods all ambulatory; mandible molar and lacinia mobilis vestigial or absent; incisor narrow; maxilla I lateral lobe arcuate; maxilla II vestigial ..... Corallanidae
3′	Pereopods with all dactyls recurved, acute; mandible molar large, angular, flat, anterior margin with "teeth"; lacinia mobilis distinct; incisor tridentate; maxilla I lateral lobe with stout spines; maxilla II developed ..... **Cirolanidae [p. 861]**

Malacostraca: Isopoda: Cymothoida: Cymothooidea: Cirolanidae: Genera

1	Eyes absent 2
1′	Eyes minute, but present; body length ≤5 mm ..... *Saharolana seurati* Monod, 1930 [Tunisia]
2(1)	Uropod with one terminal ramus, ramus length <0.25x peduncle; body length ≤5mm 3
2′	Uropod with two terminal rami, subequal in length to peduncle; body length variable 4
3(2)	One pleonite free from the pleotelson, with some sutures visible laterally for the fused segments; uropod peduncle flattened dorsoventrally ..... *Faucheria faucheri* [France]
3′	All pleonites fused completely to pleotelson with only one suture visible laterally; uropod peduncle elongate and cylindrical, with a single, minute ramus ..... *Kensleyana briani* Bruce & Herrado-Pérez, 2005 [Spain]
4(2)	Body length 1–10mm; animal not interstitial 5
4′	Body length 10–33mm ..... *Sphaeromides* [France, Balkans]
5(4)	First antennae with ≥7 flagellomeres; pleopod I not forming an operculum 6
5′	First antennae with ≤6 flagellomeres; pleopod I forming an operculum; body length ≤5 mm; animal living interstitially ..... ***Turcolana*** **[p. 861]**
6(5)	Cephalon not laterally overlapped by pereonite I 7
6′	Cephalon posterior 50% embraced by pereonite I; body length ≤7mm ..... *Marocolana delamarei* Boutin, 1993 [Morocco]

7(6) Clypeus not projecting; pleonite V overlapped by pleonite IV 8

7′ Clypeus projecting; pleonite V not overlapped by pleonite IV ..... *Metacirolana ponsi* Jaume & Garcia, 1992 [Spain]

8(7) Uropod rami dorsoventrally flattened, triangular, subequal in length to peduncle, and shorter than pleotelson ..... *Typhlocirolana* [Italy, Spain, North Africa]

8′ Uropod rami subcylindrical, styliform, length ~1.5x peduncle, longer than pleotelson ..... *Botolana leptura* (Botosaneanu, Boutin & Henry, 1985) [Morocco]

Malacostraca: Isopoda: Cymothoida: Cymothooidea: Cirolanidae: *Turcolana*: Species

Distributional data and modified keys after the excellent work of Prevorčnik et al. (2016).

1 Uropod not styliform, length ≥1.2x pleotelson 2

1′ Uropod styliform, length ~2x pleotelson, uropodal rami subequal; pleotelson posteriorly arcuate, rounded, posterior margin entire, lacking an emargination; male propodial organs on pereopods II and III ..... *Turcolana lepturoides* Prevorčnik, Konec, & Sket, 2016 [Greece, Turkey]

2(1) Pleotelson with apical emargination depth 0.06–0.1x pleotelson length 3

2′ Pleotelson apical margin entire, rarely with slight emargination 5

3(2) Pleotelson anterolateral margins convex, posterolateral margins not or weakly convergent, apical emargination wider than deep; uropod exopodite length <0.5x endopodite; propodial organs absent 4

3′ Pleotelson anterolateral margins parallel, posterolateral margins obviously convergent, apical sinus width and depth subequal; uropod exopodite slender, length >0.5x endopodite; male propodial organs on pereopods II and III ..... *Turcolana adaliae* Botosaneanu & Notenboom, 1989 [Turkey]

4(3) Uropod sympodite broad basally, medial margin not convex, medial angle not protruding beyond endopodite medial angle ..... *Turcolana pamphyliae* Botosaneanu & Notenboom, 1989 [Turkey]

4′ Uropod sympodite narrow basally, medial margin convex, medial angle protruding beyond endopodite medial angle ..... *Turcolana cariae* Argano & Pesce, 1980 [Turkey]

5(2) Pleotelson posterior margin rounded or slightly emarginate; uropod endopodite length >0.8x sympodite, rami subequal 6

5′ Pleotelson posterior margin nearly straight; uropod endopodite length ~0.6x sympodite, exopodite length ~0.6x endopodite ..... *Turcolana rodhica* Botosaneanu, Boutin & Henry, 1985 [Turkey]

6(5) Pereonal coxae II–VII clearly extending beyond respective pereonite posterior margin 7

6′ Pereonal coxae II and III not extending beyond posterior respective pereonite margin 8

7(6) Uropod length ≥0.16x body length, sympodite compact, apical width >2x basal, endopodite width ~2x exopodite width; male propodial organs pereopods ..... *Turcolana steinitzi* (Strouhal, 1961) [Israel, Lebanon]

7′ Uropod length ~0.18x body length, sympodite long, apically width <2x basal, endopodite width ≥1.8x exopodite width, tapering; propodial organs absent ..... *Turcolana smyrnae* Botosaneanu & Notenboom, 1989 [Turkey]

8(6) Uropod length 0.25x body length, sympodite length 2x width, endopodite length 3.6x width and 1.3x exopodite width; pleotelson outline variable; propodial organs absent ..... *Turcolana detecta* Botosaneanu & Notenboom, 1992 [Israel]

8′ Uropod length 0.20–0.23x body length, sympodite length ≤1.8x width, endopodite length ≤2.7x width and >1.6x exopodite width; pleotelson rounded apically; male propodial organs on pereopods II and III ..... *Turcolana reichi* (Por, 1962) [Israel, Egypt]

Malacostraca: Isopoda: Sphaeromatidae: Genera

1 Pleopods IV and V endopods lacking transverse pleats or folds 2

1′ Pleopods IV and V endopods with transverse pleats or folds; brackish water 5

2(1) Pleotelson preceded by two or more pleonites, fused at least dorsomedially 2

2′	Pleotelson preceded by two free and articulated pleonites ..... *Monolistra* [Peri-Mediterranean]
3(2)	Uropod length at least 0.5x pleotelson length 4
3′	Uropod length ~0.25x pleotelson length (known only from single pleotelson from a cave) ..... *Merozoon vestigatum* Sket, 2012 [Croatia]
4(3)	Pleotelson preceded by three pleonites fused dorsomedially ..... *Gnorimosphaeroma* [Eastern China, Japan, Korea, eastern Russia. Nearctic]
4′	Pleotelson preceded by two pleonites fused at least dorsomedially ..... *Caecosphaeroma* [Peri-Mediterranean]
5(1)	Maxilliped articles II–IV lacking lobes, inferior margins with dense fringes of finely plumose setae ..... *Sphaeroma podicipitis* Monod, 1931 [Morocco]
5′	Maxilliped articles II–IV more or less lobed, inferior margins with a fringe of simple setae ..... ***Lekanesphaera*** **[p. 863]**

Malacostraca: Isopoda: Sphaeromatidae: *Lekanesphaera*: Species

Brackishwater species. Key modified after Jacobs (1987).

1	Pereopod I propodus rostrodistal spine with few to many subtending distal setae 2
1′	Pereopod I propodus rostrodistal spine lacking subtending distal setae ..... *Lekanesphaera hookeri* Leach, 1814 [Northwest Europe]
2(1)	Pereopod I propodus rostrodistal spine with >3 setae inserted distally in transverse row; antenna flagellomeres distomedial angle with setal fringe length 2 to 3x article length ..... *Lekanesphaera panousei* (Daguerre de Hureaux, Elkaim & Lejuez, 1964) [Morocco]
2′	Pereopod I propodus rostrodistal spine with 2–3 setae inserted distally in transverse row; antenna flagellomeres distomedial angle with setal fringe length 1.5x article length ..... *Lekanesphaera rugicauda* (Leach, 1814) [Northwest Europe]

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Malacostraca: Thermosbanacea

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INTRODUCTION

Palaearctic freshwater Thermosbanaeceans are rare obligatory inhabitants of groundwater, where they are found in caves or other habitats where subterranean waters flow through unconsolidated deposits (e.g., gravel, sand, soil).

LIMITATIONS

Thermosbanaeceans are blind animals that typically live in groundwater habitats. They are delicate and easily damaged. Many species are described based on small differences in setal numbers and patterns.

TERMINOLOGY AND MORPHOLOGY

The general morphological terminology for thermosbanaeceans is not different generally from other malacostracans, unless one is working with a large number of species. In that case intimate knowledge with setal forms and characters are required. Users should consult Wagner's (1994) monograph for a full explanation of terms.

MATERIAL PREPARATION AND PRESERVATION

Thermosbanaeceans should be placed in 70% ethyl alcohol; however, 80%–95% may be required when many specimens are collected in order to prevent dilution from the animal's high body water content. Specimens are best examined in 70% ethanol and viewed under low power magnification for family, or sometimes, genus level determination. For species-level identification, microscopic dissection may be required.

KEYS TO THERMOSBAENACEA

These keys are modified after the excellent work of Wagner (1994).

Malacostraca: Thermosbaenacea: Families

1	Seven pairs of pereopods; telson not fused with pleonite VI 2
1′	Five pairs of pereopods; telson fused with pleonite VI ..... Thermosbaenidae, one species; *Thermosbaena mirabilis* Monod, 1924 [Tunisia]
2(1)	Ocular scales present; gnathopod bearing two or three serrate macrosetae; gnathopod propodus lacking a "spur"; pleopod I a minute lobe (Fig. 16.6.16 B) ..... Halosbaenidae, one species; *Limnosbaena finki* (Mestrov & Lattinger-Penko, 1969) [Bosnia-Herzegovina; Italy]
2′	Ocular scales absent; gnathopod bearing one serrate macroseta; gnathopod propodus bearing a "spur"; pleopod I articulating basally ... . Monodellidae, one genus: ***Tethysbaena*** **[p. 864]**

Malacostraca: Thermosbaenacea: *Tethysbaena*: Species

1	Telson length > width; anal lobes not projecting beyond telson distal margin 3
1′	Telson width > length; anal lobes projecting beyond telson distal margin ..... *Tethysbaena relicta* (Pór, 1962) [Israel]
2(1)	Maxilla II basipodal endite II with 17 macrosetae bearing a distal pecten; telson mean width: length ratio 0.98 .... *Tethysbaena atlantomaroccana* Cals & Boutin, 1885 [Morocco]
2′	Maxilla II basipodal endite II with 25 macrosetae bearing a distal pecten; telson mean width: length ratio 0.95 .... *Tethysbaena tarsiensis* Wagner, 1994 [Spain]

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Malacostraca: Decapoda

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INTRODUCTION

The freshwater and terrestrial decapods of the Palaearctic are treated. All terrestrial species may be often found in and around freshwater, especially younger individuals. The Palaearctic has few native crayfish, most of which are rare or endangered and generally protected under law. Several invasive crayfish have been introduced through the aquarium trade and aquaculture.

LIMITATIONS

In general, sexually mature individuals (most frequently males) are required for species-level identifications. In almost all crayfish and crabs, fully mature males are required for any meaningful identifications. Females and juvenile males cannot be identified with reasonable accuracy for the Cambaridae, Potamidae, and Gecarcinucidae. Identifying caridean shrimp is very difficult, and the admonition of Jugovic et al. (2010) should be heeded. That is, only mature specimens, and frequently only males, can be identified, and size is not a reliable indication of maturity. Many genera need to be revised and new taxa are still being discovered and described particularly from cave systems, and in Asia, close to the tropical regions.

The greatest limitation, however, is that many shrimp, crab, and crayfish are introduced to new areas, typically as escaped or released bait, as aquarium specimens, or for aquaculture.

TERMINOLOGY AND MORPHOLOGY

The keys are mostly based on morphological characters, although molecular (DNA) characters sometimes supplement morphology or even replace them for species that have been analyzed phylogenetically but remain morphologically understudied. Decapods are in part defined by their name: Decapoda, or "ten legs." The first or second pair of pereopods (walking limbs) may be chelate (modified as pinchers), or modified for filter feeding, by possessing elongated **setal fans**.

The **carapace** is the dorsal shield that covers the animal. Anteriorly, the carapace may project between the eyes as a **rostrum** in shrimp and crayfish, or as the **front** in crabs. In shrimp, the presence, number, and position of spiniform **teeth** on the rostrum is important, as are presence or absence of specific spines on the carapace surface (Fig. 16.6.16 B): the **supraorbital spine** (above and just posterior to the eye), the **suborbital spine** (just below the eye), the **hepatic spine** (on the side of the carapace, posterior to the eye, and at least the length of the eye stalk away from the eye), the **branchostegial spine** (between the eye and the ventral margin of the carapace, set back posteriorly from the anterior carapace margin), and the **pterygostomial spine** (at the anterolateral corner of the carapace). The aforementioned carapace anterolateral corner is the **pterygostomial angle**, and may be rounded, produced, or acute, with or without a spine.

On the dorsal surface of the crayfish carapace, behind the medial arc of the cervical groove, are paired longitudinal, parallel lines (called the **branchiocardic grooves**) that arc toward each other medially. The region between them is the **areola**, which may be obliterated if the lines come together. Generally the areola is open and contains **punctations**, which are very small, shallow, usually circular depressions. The length and width of the areola, and sometimes the number of punctations are diagnostic characters.

Decapods bear five pairs of **pereopods** (ambulatory limbs; Fig. 16.6.16 C), with the first and sometimes the second pair modified as **chelae** (claws). Each pereopod is composed of several podomeres, which are (from basal most to distal most: **coxa**, **basis**, **ischium**, **merus**, **carpus**, **propodus,** and **dactylus**). The coxae and ischia may bear diagnostic structures in the form of **bosses** or **hooks**. A **chela** claw is composed of the propodus and the dactylus. The propodus is comprised of the broad **palm** and a distal extension called the **pollex** (or fixed "finger"). The dactylus is the "movable finger" that moves against the pollex. The opposing margins of the dactylus and pollex may have defining characters in terms of gape or tubercle arrangement.

The chelae are important in species diagnoses; however, decapods commonly lose and regenerate them. Chelae characteristics used in this key apply only to non-regenerated chelae. Regenerated chelae differ from non-regenerated in that they possess tubercles of the same size along the opposable margins of the dactyl and pollex, as well as by having a much shorter palm region.

Atyid shrimps are characterized by modified chelae of the first two pairs of pereopods. These bear thick bands of setae along the dactyl and propodus distal margins

(Fig. 16.6.16 E), thereby composing a filtering or scraping apparatus when the chela is open. The carpus in both pairs of pereopods is modified to receive the propodus.

The limb may have an elongate structure from the top of the ischium called an **exopod** (Fig. 16.6.16 C). A gill may grow from the coxa called a **podobranch**. If the gill grows from the body at the point of the limb attachment, then it is called an **arthrobranch**. If the gill grows from the body above the point of limb attachment, it is called a **pleurobranch**.

The abdomen is posterior to the carapace and may be flat folded beneath the body (crabs) or projecting posteriorly (shrimp, crayfish). The **pleopods** depend from the ventral surface of the abdomen. The abdomen terminates in a **telson**, which has a **uropod** on either side. The pleopods and the uropods are generally biramal, with a basal **peduncle**, which bears two branches: the lateral **exopod** and the medial **endopod**. Male shrimp frequently have the endopod of the first and second pleopod further divided into a lateral lamella, an **appendix masculina** and a lateral **appendix interna**. The uropod has an oblique suture across the distal third or so of the exopod, called a **diaresis**.

The primary identification characters for many species are on the male **gonopods**; these are the first one or two pleopod pairs that have been modified for sperm transfer. As the external morphology of freshwater crabs is relatively conservative, the keys place greater emphasis on the taxonomically important gonopod I (first pleopod) and gonopod II (second pleopod) of mature male individuals. It should be noted that there are some differences in published taxonomic literature with regard to terminology used to refer to parts/sections of gonopod I. In most of the freshwater crab taxonomic literature, the often conspicuous distal part or apex of gonopod I and the adjacent subdistal part—together forming the anatomical third article of gonopod I (Smalley, 1964; Brandis et al., 1999)—are respectively referred to as "terminal" and "subterminal" segments (e.g., Yeo & Ng, 2007) or "distal"' and "subdistal" segments (e.g., Dai, 1999). Other studies, taking into consideration the actual anatomy of the gonopod I, refer to them instead as "terminal"' and "subterminal joints" (e.g., Brandis et al., 2000). There is no consensus on the terminology that should be applied. Hence, for now these terms are used interchangeably in the different keys of this chapter, with some modification—"terminal" and "subterminal joint" are replaced by "terminal article" and "subterminal" part of the gonopod I, respectively, to avoid the disambiguation of "joint" with "articulation," and "segment" is replaced by "article" since, in actuality, the term "segment" should only be used for body sections (somites). Therefore in this chapter, distal article = terminal article (= terminal joint or terminal segment); and subdistal article = subterminal part of gonopod I (= subterminal joint or subterminal segment).

MATERIAL PREPARATION AND PRESERVATION

Decapods are best preserved in ethyl alcohol. The gonopod is typically dissected out and examined separately. Generally, the gonopod may be temporarily mounted on an insect pin for easy manipulation under the microscope. The gonopod is then generally kept in a smaller vial within the jar holding the larger specimen.

KEYS TO DECAPODA

Malacostraca: Decapoda: Infraorders

1	Abdomen projecting posteriorly (Fig. 16.6.18)	2
1′	Abdomen folded beneath body, tightly pressed to thorax (Fig. 16.6.10)	**Brachyura [p. 866]**
2(1)	Abdomen compressed laterally; abdominal pleuron II overlapping pleura I and III	**Caridea [p. 876]**
2′	Abdomen compressed dorsoventrally; abdominal pleuron II not overlapping pleura I and III	**Astacidea [p. 879]**

Malacostraca: Decapoda: Brachyura: Families

1	Carapace in dorsal view ovate to quadrangular, rostrum absent	2
1′	Carapace in dorsal view subcircular, bearing a rostrum	Hymenosomatidae, one genus: ***Neorhynchoplax*** **[p. 867]**
2(1)	Carapace front (space between eyes) at least one-third of carapace anterior width	3
2′	Carapace front less than one-third carapace anterior width (fiddler crabs)	**Ocypodidae [p. 867]**
3(2)	Maxillipeds III, medial margins emarginate or indented, forming distinct rhomboidal or diamond-shaped gap between them	4
3′	Maxillipeds III, medial margins straight, parallel, without rhomboidal or diamond-shaped gap between them	5

4(3) Maxiliped III merus and ischium with clear, oblique, setose ridge; pterygostomian region with setae in reticulated pattern of evenly and densely spaced short stiff setae; oral region with a rhomboidal gap between third maxillipeds ..... Sesarmidae, one genus; ***Sesarmops*** **[p. 867]**

4′ Maxiliped III merus and ischium without clear, oblique, setose ridge; pterygostomian region with scattered setae, not set in reticulated pattern; oral region with diamond-shaped gap between third maxillipeds ..... **Varunidae [p. 867]**

5(2) Mandibular palp with two articles, terminal palpomere bilobed ..... **Gecarcinucidae [p. 868]**

5′ Mandibular palp with three articles, terminal palpomere simple ..... **Potamidae [p. 868]**

Malacostraca: Decapoda: Brachyura: Hymenosomatidae: *Neorhynchoplax*: Species

1 Pereopod III length 1.4−1.7x carapace width ..... *Neorhynchoplax kempi* (Chopra & Das, 1930) [Iraq]

1′ Pereopod III length 1.9−2.5x carapace width ..... *Neorhynchoplax introversa* (Kemp, 1917) [China]

Malacostraca: Decapoda: Brachyura: Ocypodidae: Genera

Modified from Shih et al. (2016a).

1 Orbital floor without tubercle; carapace without tubercles, but striae may be present 2

1′ Orbital floor with tubercle adjacent to antenna I; carapace covered in tubercles; up to 1.5 km upstream from the sea ..... *Afruca tangeri* (Eydoux, 1835) [Morocco, Portugal, Spain(?). Atlantic Afrotropical]

2(1) Front width >2x one eyestalk base 3

2′ Front width ≤1.5x one eyestalk base; muddy river mouths, brackish and marine ..... *Tubuca acuta* (Stimpson, 1858) [China, Japan, Korea. Australian, Oriental]

3(2) Major cheliped dactylus bearing large, subdistal tubercle; major manus lateral surface with scattered tubercles; rare in brackish, coastal streams ..... *Cranuca inversa* (Hoffman, 1874)

3′ Major cheliped dactylus without large, subdistal tubercle; major manus lateral surface smooth; rare in brackish, coastal streams ..... ***Austruca*** **[p. 867]**

Malacostraca: Decapoda: Brachyura: Ocypodidae: *Austruca*: Species

1 Carapace anterolateral angles triangular; major pollex gape without or with small predistal triangular tubercle; gonopod I with posterior flange longer, broader than anterior ..... *Austruca lactea* (De Haan, 1835) [China, Japan. Oriental]

1′ Carapace anterolateral angles strongly acute; major pollex gape with small to moderate predistal triangular tubercle; gonopod I with anterior flange longer, broader than posterior ..... *Austruca annulipes* (H. Milne Edwards, 1837) [Coastal Arabian Peninsula, Iraq. Afrotropical, Oriental]

Malacostraca: Decapoda: Brachyura: Sesarmidae: *Sesarmops*: Species

1 Carapace breadth between external orbital angles ≥ carapace length; carapace lateral borders diverging posteriorly; coastal rivers and streams, semiterrestrial ..... *Sesarmops impressus* (H. Milne Edwards, 1837) [China, Japan]

1′ Carapace breadth between external orbital angles > carapace length; carapace lateral borders subparallel; coastal rivers and streams, semiterrestrial ..... *Sesarmops sinensis* (H. Milne Edwards, 1853) [China. Afrotropical, Australian, Oriental]

Malacostraca: Decapoda: Brachyura: Varunidae: Genera

1 Maxilliped III exopodite width < ischium width 2

1′ Maxilliped III exopodite width = ischium width ..... *Ptychognathus* [China, Japan. Oriental]

2(1) Chelae palmar lateral surface glabrous; posterior pereopods with dactyli densely fringed along both margins in long natatory setae ..... ***Varuna*** [China, Japan, Indian Ocean coastal rivers. Afrotropical, Australian, Oriental]

2′ Chelae palmar lateral surface densely tomentose; posterior pereopods with dactyli fringed proximally with loose, flexible setae, and distally glaborous (Fig. 16.6.7) ..... ***Eriocheir*** [Widespread]

Malacostraca: Decapoda: Brachyura: Varunidae: *Varuna*: Species

1 Carapace first anterolateral tooth truncated; gonopod I apically trilobed ..... *Varuna yui* Hwang & Takeda, 1986 [China. Oriental]

1′ Carapace first anterolateral tooth rounded; gonopod I apically bilobed ..... *Varuna litterata* (Fabricius, 1798) [China, Japan. Afrotropical, Oriental]

Malacostraca: Decapoda: Brachyura: Varunidae: *Eriocheir*: Species

1 Carapace anterior margin between eyes sinuate, with four low, rounded lobes ..... *Eriocheir japonica* (De Haan, 1835) [China, Japan, Korea, Russia. Oriental]

1′ Carapace anterior margin between eyes with four acute projections (Fig. 16.6.8) ..... *Eriocheir sinensis* H. Milne Edwards, 1853 [China, Korea. Invasive in Europe, Caspian Sea, elsewhere]

Malacostraca: Decapoda: Brachyura: Gecarcinucidae: Genera

1 Carapace anterolateral margin with epibranchial tooth positioned more or less in line with postorbital crista; maxilliped III ischium lacking longitudinal median sulcus; cheliped merus dorsal margin lacking subterminal spine; male abdomen triangular ..... ***Sodhiana*** **[p. 868]**

1′ Carapace anterolateral margin with epibranchial tooth positioned much posteriorly to postorbital crista; maxilliped III ischium with distinct longitudinal median sulcus; cheliped merus dorsal margin with distinct subterminal spine; male abdomen distinctly T-shaped ..... ***Sartoriana*** **[p. 868]**

Malacostraca: Decapoda: Brachyura: Gecarcinucidae: *Sodhiana*: Species

1 Gonopod I terminal article apex straight or gently bent or curved laterally 2

1′ Gonopod I terminal article with apex gently bent or curved medially..... *Sodhiana iranica* Sharifian, Kamrani, & Sharifian, 2014 [Iran]

2(1) Gonopod I subterminal article more or less straight, with only indistinct to very weak bend/angle on lateral margin 3

2′ Gonopod I subterminal article bent laterally, with distinct obtuse bend/angle on lateral margin at one third length from base ..... *Sodhiana rokitanskyi* (Pretzmann, 1971) [Iran]

3(2) Gonopod I terminal article with lateral and medial margins very gently convex and very gently concave, respectively, apex subtruncate ..... *Sodhiana afghaniensis* (Pretzmann, 1963) [Afghanistan]

3′ Gonopod I terminal article with lateral and medial margins straight, apex subacute ..... *Sodhiana blanfordi* (Alcock, 1909) [Pakistan]

Malacostraca: Decapoda: Brachyura: Gecarcinucidae: *Sartoriana*: Species

1 Carapace subquadrate, anterolateral and posterolateral margins gently converging anteriorly and posteriorly, respectively; anterolateral margin between lateral orbital angle and epibranchial tooth produced as broad lobe, with narrow, acute cleft separating epibranchial tooth from anterolateral margin; postorbital cristae almost straight; branchial regions relatively flat ..... *Sartoriana trilobata* Alcock, 1909 [India: Assam]

1′ Carapace distinctly transverse, anterolateral and posterolateral margins strongly converging anteriorly and posteriorly, respectively; anterolateral margin between external orbital angle and epibranchial tooth convex but not produced as lobe, with broad cleft separating epibranchial tooth from anterolateral margin; postorbital cristae gently sinuous; branchial regions strongly convex ..... *Sartoriana spinigera* (Wood-Mason, 1871) [India, Nepal, Pakistan. Oriental]

Malacostraca: Decapoda: Brachyura: Potamidae: Genera

1 Male sternites VII and VIII separated by transverse ridge, interrupting median line (Fig. 16.6.61) ..... (subfamily Potaminae) 2

1′ Male sternites VII and VIII without transverse ridge (Fig. 16.6.62) (subfamily Potamiscinae) 4

2(1) Carapace anterolateral margin with 0 or 1 epibranchial tooth 3

2′ Carapace anterolateral margin with 3–4 prominent epibranchial teeth ..... ***Paratelphusula*** **[p. 869]**

3(2) Epigastric cristae almost level with or slightly anterior to postorbital cristae, with edges not overlapping; occurs east of the Indus River ..... ***Himalayapotamon*** **[p. 871]**

3′ Epigastric cristae distinctly anterior to postorbital cristae, with outer edge overlapping inner edge of postorbital cristae; occurs west of the Indus River ..... ***Potamon*** **[p. 869]**

4(1) Maxilliped III exopod with flagellum absent or vestigial 5

4′ Maxilliped III exopod with long, with well-developed flagellum 6

5(4) Carapace surface with minute folds; maxilliped III exopod with terminal setae, flagellum absent; gonopod I distal article length >0.7x subdistal article ..... ***Aparapotamon*** **[p. 872]**

5′ Carapace surface smooth; maxilliped III exopod lacking terminal setae, flagellum absent or vestigial; gonopod I distal article length up to 0.6x subdistal article ..... ***Potamiscus*** **[p. 872]**

6(4) Carapace dorsal surface relatively convex; male abdomen relatively broad 7

6′ Carapace dorsal surface relatively flat; male abdomen relatively narrow ..... ***Tenuilapotamon*** **[p. 873]**

7(5) Epigastric and postorbital cristae distinct; gonopod I stout, terminal article stout, with distal part tapered toward broadly rounded or truncate tip; gonopod II distal article length ~0.5x basal article 8

7′ Epigastric and postorbital cristae indistinct or absent; gonopod I slender, terminal article slender, gently tapered distally to acute tip; gonopod II distal article length <0.5x basal article ..... ***Geothelphusa*** **[p. 873]**

8(7) Gonopod I apex reaching beyond abdominal lock tubercle, terminal article directed distolaterally, subterminal article flap extending medially ..... ***Sinopotamon*** **[p. 873]**

8′ Gonopod I apex not reaching abdominal lock tubercle, terminal article directed dorsomedially, subterminal article flap extending subdistally ..... ***Longpotamon*** **[p. 874]**

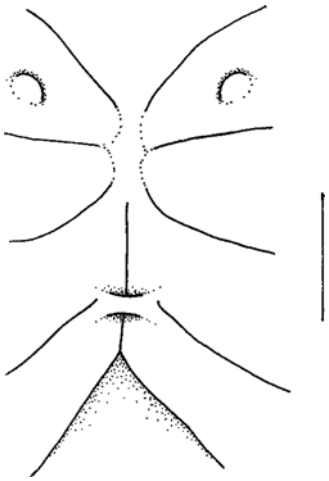


FIGURE 16.6.61 Male posterior thoracic sternum of *Potamon fluviatile* (Potaminae) demonstrating sternites VII and VIII separated by a transverse ridge, interrupting the median line. Scale bar = 2 mm. *After Yeo & Ng (2003).*

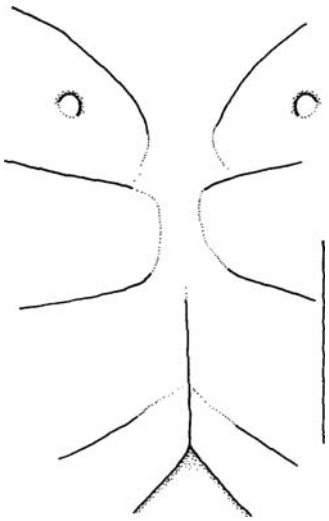


FIGURE 16.6.62 Male posterior thoracic sternum of *Eosamon smithianum* (Potaminae) demonstrating sternites VII and VIII without a transverse ridge. Scale bar = 5 mm. *After Yeo & Ng (2003).*

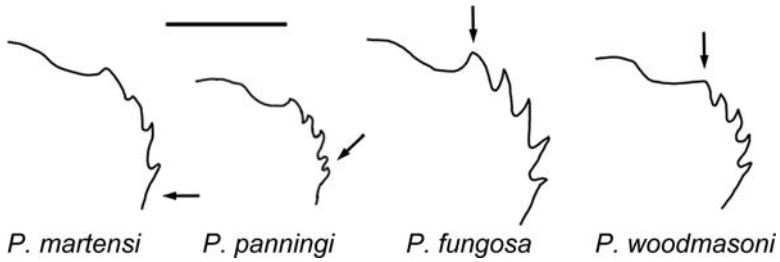


FIGURE 16.6.63 Anterolateral margin of the Himalayan/North Indian representatives of the genus *Paratelphusula sensu lato*. Arrows point at diagnostic characters. Scale bar = 1 cm. *After Klaus et al. (2017).*

Malacostraca: Decapoda: Brachyura: Potamidae: Potaminae: *Paratelphusula*: Species

This key is based exclusively on the shape of the carapace anterolateral margin (Fig. 16.6.63), and only includes the four species from Northern India, Nepal, and Bhutan.

1	Anterolateral margin with four epibranchial teeth 2
1′	Anterolateral margin with three epibranchial teeth ..... *Paratelphusula martensi* Wood-Mason, 1875 [Bhutan, India, Nepal. Oriental]
2(1)	Anterolateral teeth three and four acute, not closely together 3
2′	Anterolateral teeth three and four small, blunt, close set; small animals ..... *Paratelphusula panningi* (Bott, 1966) [India, Nepal. Oriental]
3(2)	External orbital angle directed anteriorly ..... *Paratelphusula fungosa* (Alcock, 1909) [India: Assam. Oriental]
3′	External orbital angle blunt, not directed anteriorly ..... *Paratelphusula woodmasoni* (Rathbun, 1905) [India: Assam. Oriental]

Malacostraca: Decapoda: Brachyura: Potamidae: Potaminae: *Potamon*: *S*pecies

This key is based on Brandis et al. (2000), including their system of four subgenera, and relies primarily on the morphology of the male first gonopod. Decisive characters of the gonopod I are the shape of its terminal article and the shape of the flexible zone on the dorsal side that separates the terminal article from the subterminal part. In case cytochrome oxidase subunit 1 (CO1) gene nucleic acid sequence differences are applied, the nucleotide position is counted from the first base of the start codon on the coding strand.

The key includes species described since Brandis et al. (2000), as well as previously synonymized species (see Jesse et al. 2011), with a total number of 22 species. We thank Reza Naderloo and Alireza Keikhosravi for providing gonopod I images of several Iranian species.

1	Gonopod I with terminal article broad, more or less oval; mesial portion distinctly tumid; apex long, slightly curved (Fig. 16.6.64) ..... 2 [Western Mediterranean drainages]
1’	Gonopod I with terminal article conical or slender; mesal part not tumid (Fig. 16.6.64) 4
2(1)	Gonopod I flexible zone V-shaped (Fig. 16.6.64) 3
2′	Gonopod I flexible zone distinctly bilobed (Fig. 16.6.64) ..... *Potamon* (*Eutelphusa*) *algeriense* Bott, 1967 [Algeria, Morocco, Tunisia]
3(2)	CO1 gene with guanine bases at positions 129, 150; cytosine at positions 195, 261; thymine at positions 120, 192 ..... *Potamon* (*Eutelphusa*) *fluviatile* (Herbst, 1785) [Albania, Croatia, Greece, Italy, Macedonia, Malta, Montenegro]
3′	CO1 gene with cytosine at positions 120, 192; adenine at positions 150; thymine at positions 129, 195, 261 ..... *Potamon* (*Euthelphusa*) *pelops* Jesse, Schubart, & Klaus, 2011 [Greece; Peloponnesus]
4(1)	Gonopod I terminal article very slender, fusiform (Fig. 16.6.64) ..... 5 [Aegean, Black and Caspian Seas drainages]
4′	Gonopod I terminal article conical, cylindrical or triangular (Fig. 16.6.64) [river systems draining toward the Eastern Mediterranean and further east] 7
5(4)	Gonopod I flexible zone broad, or only narrowed in its lateral part 6
5′	Gonopod I flexible zone very narrow (Fig. 16.6.64) ..... *Potamon* (*Pontipotamon*) *bilobatum* Brandis, Storch & Türkay, 2000 [Iran]
6(5)	CO1 gene with adenine bases at positions 114, 303; cytosine at positions 138, 192; thymine at positions 84 ..... *Potamon* (*Pontipotamon*) *ibericum* (Bieberstein, 1808) [Northern Aegean, Black and Caspian Seas drainages]

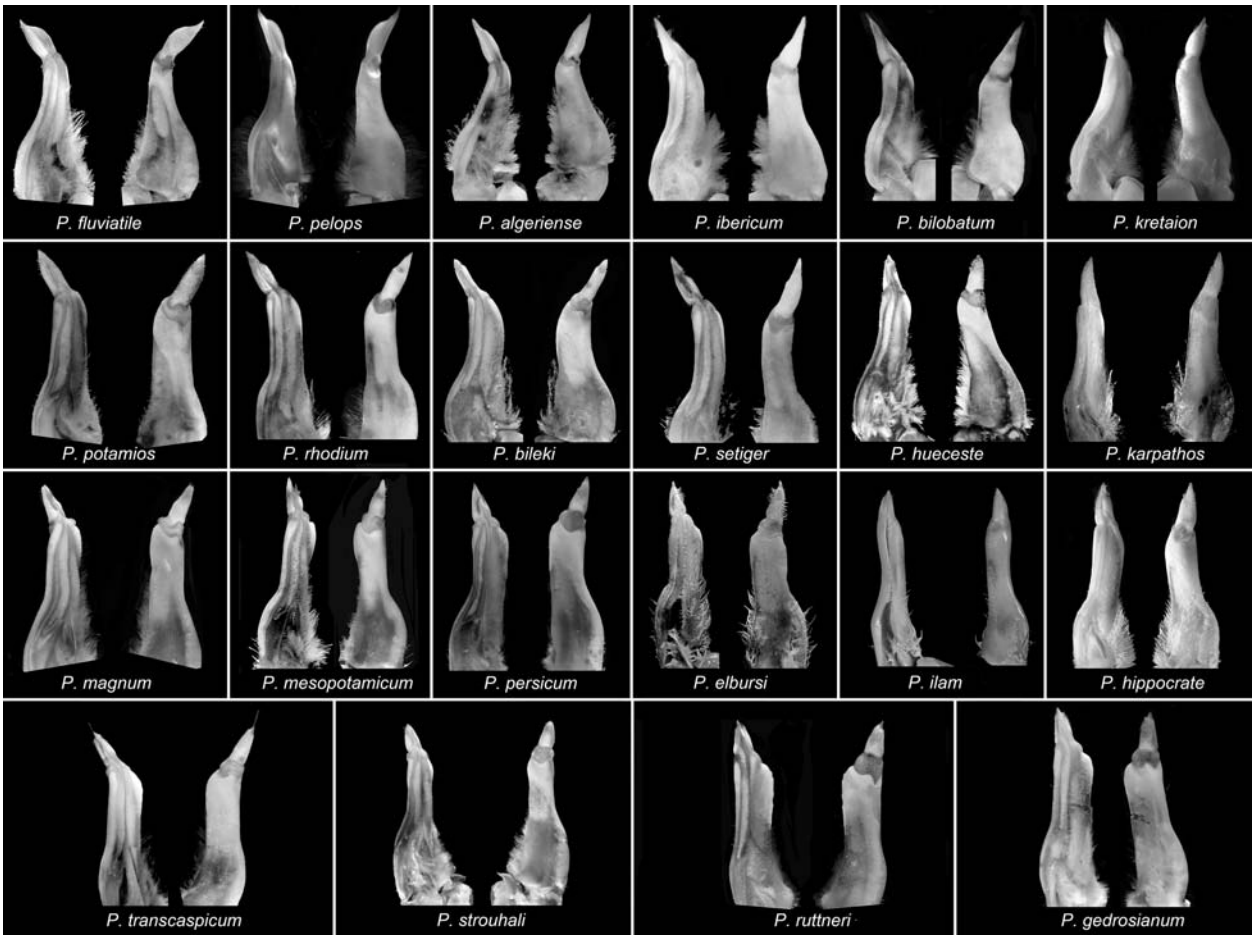


FIGURE 16.6.64 First gonopods (G1) of *Potamon* species in ventral (left) and dorsal (right) view. Different scales.

6′ CO1 gene with guanine bases at positions 114, 303; thymine at positions 138, 192; cytosine at position 84 ..... *Potamon* (*Pontipotamon*) *kretaion* Giavarini, 1934 [Greece: Crete]

7(4) Gonopod I terminal article elongated and conical, mesial edge slightly bulging (Fig. 16.6.64) ..... 8 [Eastern Mediterranean drainages]

7′ Gonopod I terminal article stout and triangular; subterminal part with projecting mesial edge (fig. 16.6.64) ..... 13 [Euphrates and Tigris drainages]

8(7) Gonopod I flexible zone not symmetrically bilobed (Fig. 16.6.64) 9

8′ Gonopod I flexible zone symmetrically bilobed (Fig. 16.6.64) 11

9(8) Gonopod I flexible zone not distinctly V-shaped (Fig. 16.6.64) 10

9′ Gonopod I flexible zone distinctly V-shaped (Fig. 16.6.64) ..... *Potamon* (*Potamon*) *rhodium* Parisi, 1913 [Greece, Turkey]

10(9) Gonopod I flexible zone with only one linguiform elongate lobe (Fig. 16.6.64) ..... *Potamon* (*Potamon*) *setiger* Rathbun, 1904 [Syria, Turkey]

10′ Gonopod I flexible zone slender, terminal article subcylindrical and narrow (Fig. 16.6.64) ..... *Potamon* (*Potamon*) *bileki* Pretzmann, 1971 [Turkey]

11(8) CO1 gene with cytosine at positions 180, 327; thymine at positions 210, 253, 375 12

11′ CO1 gene with adenine bases at position 375; cytosine at positions 210, 253; thymine at positions 180, 327 ..... *Potamon* (*Potamon*) *karpathos* Giavarini, 1934 [Greece, Turkey]

12(9) CO1 gene with adenine base at positions 174; cytosine at position 219; guanosine at position 303 ..... *Potamon* (*Potamon*) *potamios* (Olivier, 1804) [Jordan River, Turkey]

12′ CO1 gene with adenine base at position 303; cytosine at position 174, 315; thymine at position 219 ..... *Potamon* (*Potamon*) *hippocratis* Ghigi, 1929 [Cyprus, Greece, Turkey]

13(7) Gonopod I flexible zone bilobed (Fig. 16.6.64) 14

13′ Gonopod I flexible zone V-shaped or with one mesial or lateral lobe (Fig. 16.6.64) 17

14(13) Gonopod I terminal article triangular, with nearly straight margins (Fig. 16.6.64) 15

14′ Gonopod I terminal article asymmetric in shape, mesial margin bulging in its proximal half (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *magnum* Pretzmann, 1962 [upper Tigris and its tributaries]

15(14) Gonopod I subterminal part distally with distinctly projecting mesial edge (Fig. 16.6.64) 16

15′ Gonopod I subterminal part distally rounded, without any mesial projecting edge, terminal article very stout (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *strouhali* Pretzmann, 1962 [Iran]

16(15) Gonopod I flexible zone with distinctly elongated lateral lobe, mesial lobe reduced (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *ruttneri* Pretzmann, 1962 [Afghanistan, Iran]

16′ Gonopod I flexible zone with distinctly elongated mesial lobe (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *gedrosianum* Alcock, 1909 [Afghanistan, Pakistan]

17(13) Gonopod I flexible zone distinctly V-shaped (Fig. 16.6.64) 18

17′ Gonopod I flexible zone with one mesial or laterally located lobe (Fig. 16.6.64) 21

18(17) Gonopod I subterminal part with long and projecting mesial edge; carapace anterolateral margin broad, serrated with unequal larger teeth (Fig. 16.6.64) 19

18′ Gonopod I subterminal part with short mesial projecting edge; carapace anterolateral margin distinct, but narrow, serrated with very small regular teeth (Fig. 16.6.64) 20

19(18) Gonopod I terminal article nearly triangular ..... *Potamon* (*Orientopotamon*) *mesopotamicum* Brandis, Storch & Türkay, 1998 [Euphrates, downstream Lake Assad, including Khabur River]

19′ Gonopod I terminal article conical ..... *Potamon* (*Orientopotamon*) *ilam* Keikhosravi & Schubart, 2014 [Iran]

20(18) Gonopod I terminal article proximal half with straight mesial margins, in distal half becoming sharply deflected (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *persicum* Pretzmann, 1962 [Iran, Iraq, Turkey]

20′ Gonopod I terminal article with mesial margins lacking sharp deflection (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *elbrusi* Pretzmann, 1962 [Caspian Sea drainage, Namak Lake drainage]

21(17) Gonopod I flexible zone with one lateral linguiform elongated lobe; gonopod I subterminal part with low mesial edge (Fig. 16.6.64) ... *Potamon* (*Orientopotamon*) *hueceste* Pretzmann, 1962 [Turkey]

21′ Gonopod I flexible zone with one mesial broad lobe, lateral lobe absent; gonopod I subterminal part with rounded mesial margin (Fig. 16.6.64) ..... *Potamon* (*Orientopotamon*) *transkaspicum* Pretzmann, 1962 [Caspian Sea]

Malacostraca: Decapoda: Brachyura: Potamidae: Potaminae: *Himalayapotamon*: Species

Himalayapotamon Pretzmann, 1966, is poorly known and in need of revision. This key is based on Pati & Singh (2017).

1 Male abdominal somite VI short, median length ~0.4x proximal width (Fig. 16.6.65 A, B) 2

1′ Male abdominal somite VI long, median length ≥0.5x proximal width (Fig. 16.6.65 C–E) 3

2(1) Gonopod I terminal article relatively stout, conical (Fig. 16.6.65 F) ..... *Himalayapotamon bifarium* (Alcock, 1909) [?India. Oriental]

2′ Gonopod I terminal article relatively slender,sinuate (Fig. 16.6.65 G) ..... *Himalayapotamon monticola* (Alcock, 1910) [India. Oriental]

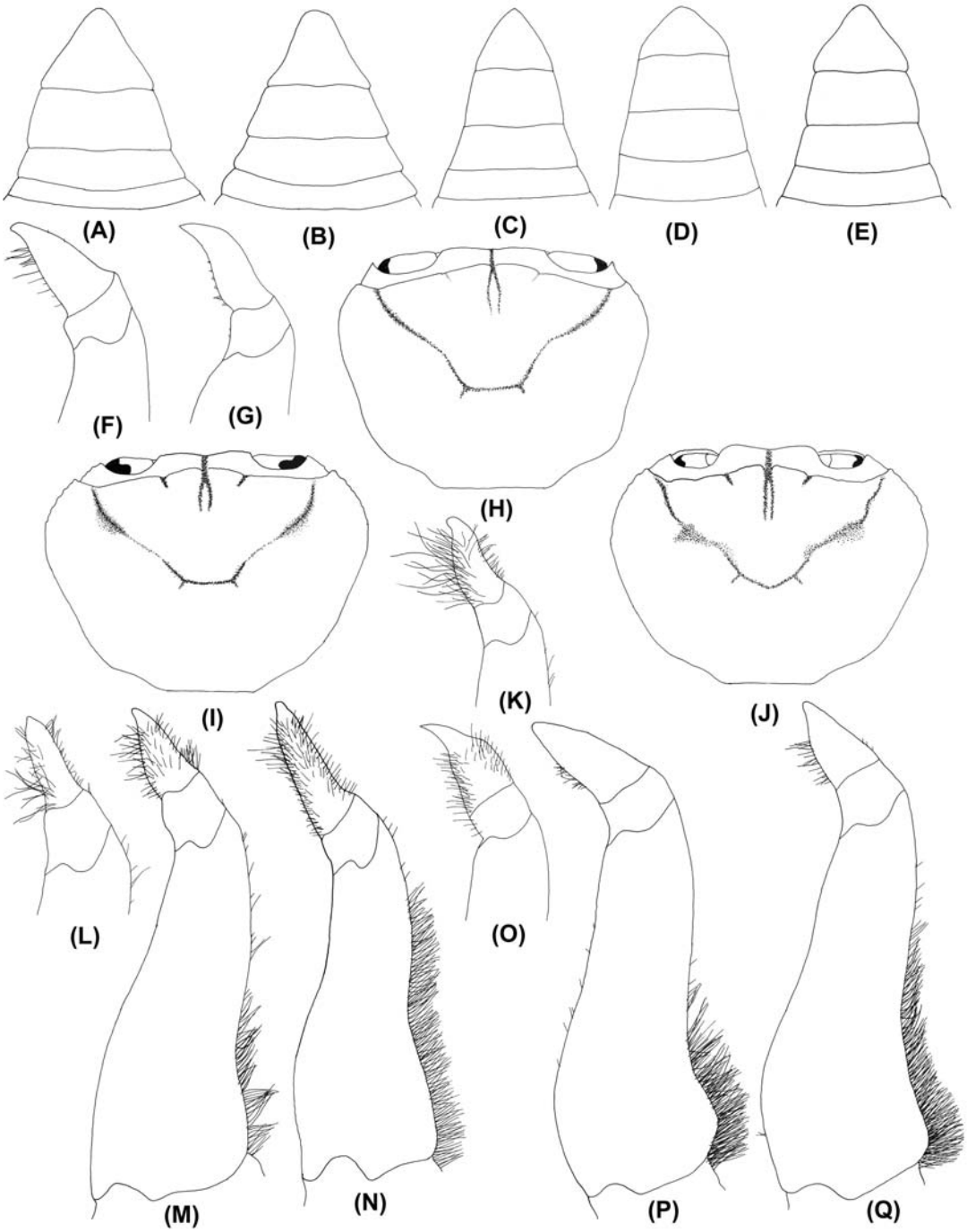


FIGURE 16.6.65 Species of *Himalayapotamon* Pretzmann, 1966: (A and F) *H. bifarium*; (B and G) *H. monticola*; (C) *H. kasaulis*; (D, I, and P) *H. marinellii*; (E, J, and Q) *H. garhwalense*; (H) *H. ambivium*; (K) *H. atkinsonianum*; (L) *H. emphyseteum*; (M) *H. koolooense*; (N) *H. sunkoshiense*; (O) *H. babaulti*. (A–E) male abdominal somites 4–6 and telson; (F, G, K, L, and O) dorsal view of left G1 terminal article; (H–J) dorsal view of carapace; (M, N, P, and Q) dorsal view of left G1.

3(1)	Male telson apex rounded (Fig. 16.6.65 D, E) 4
3′	Male telson apex acute (Fig. 16.6.65 C) ..... *Himalayapotamon kasaulis* (Pretzmann, 1966) [India: Himachal Pradesh]
4(3)	Groove separating epigastric and postorbital cristae distinct (Fig. 16.6.65 I, J) 5
4′	Groove separating epigastric and postorbital cristae indistinct (Fig. 16.6.65 H) ..... *Himalayapotamon ambivium* (Alcock, 1909) [India: Himachal Pradesh]
5(4)	Gonopod I terminal article conical, nearly straight (Fig. 16.6.65 L–Q) 6
5′	Gonopod I terminal article sinuous (Fig. 16.6.65 K) ..... *Himalayapotamon atkinsonianum* (Wood-Mason, 1871) [Bhutan, India, Nepal. Oriental]
6(5)	Gonopod I terminal article relatively slender (Fig. 16.6.65 L–N) 7
6′	Gonopod I terminal article relatively stout (Fig. 16.6.65 O–Q) 9
7(6)	Gonopod I terminal article distally narrowing toward tip (Fig. 16.6.65 M, N) 8
7′	Gonopod I terminal article distally blunt toward tip (Fig. 16.6.65 L) ..... *Himalayapotamon emphyseteum* (Alcock, 1909) [India, Nepal. Oriental]
8(7)	Gonopod I terminal article length ~0.3× subterminal part (Fig. 16.6.65 M) ..... *Himalayapotamon koolooense* (Rathbun, 1904) [Afghanistan, India, Nepal. Oriental]
8′	Gonopod I terminal article length ~0.4× subterminal part (Fig. 16.6.65 N) *Himalayapotamon sunkoshiense* Brandis & Sharma, 2005 [Nepal]
9(6)	Gonopod I terminal article with distal portion gradually tapered (Fig. 16.6.65 P, Q) 10
9′	Gonopod I terminal article with distal portion suddenly tapered (Fig. 16.6.65 O) ..... *Himalayapotamon babaulti* (Bouvier, 1918) [India: Himachal Pradesh]
10(9)	Postorbital cristae nearly straight (Fig. 16.6.65 I); male telson with straight lateral margins (Fig. 16.6.65 D); gonopod I terminal article length ~0.3x combined length of subterminal part and flexible zone (Fig. 16.6.65 P) ..... *Himalayapotamon marinellii* (Pretzmann, 1963) [India. Oriental]
10′	Postorbital cristae distinctly curved (Fig. 16.6.65 J); male telson with concave lateral margins (Fig. 16.6.65 E); gonopod I terminal article length ~0.2x combined length of subterminal part and flexible zone (Fig. 16.6.65 Q) ..... *Himalayapotamon garhwalense* Pati & Singh, 2017 [India: Uttarakhand]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Aparapotamon*: Species

The following key is modified from Dai (1999).

1	Carapace external orbital angle and/or anterolateral margin with several teeth/tubercles 2
1′	Carapace external orbital angle and/or anterolateral margin without any teeth/tubercles 4
2(1)	External orbital angle without teeth or tubercles, anterolateral margin with numerous small teeth 3
2′	External orbital angle with 5–7 tubercles, anterolateral margin with 15–17 teeth ..... *Aparapotamon muliense* Dai, Chen. Liu, Luo, Yi, Liu, Gu, & Liu, 1990 [China]
3(2)	Carapace anterolateral margin with 21 or 22 teeth; gonopod I with subdistal article length 1.5x distal article ..... *Aparapotamon grahami* (Rathbun, 1931) [China]
3′	Carapace anterolateral margin with 24–26 teeth; gonopod I with subdistal article length 1.2x distal article ..... *Aparapotamon gracilipedum* (Chen & Chang, 1982) [China]
4(1)	Gonopod I apex reaching beyond sternite VI; vulva positioned at suture between sternites V and VI ..... *Aparapotamon emineoforaminum* Dai & Chen, 1985 [China]
4′	Gonopod I apex almost reaching to anterior margin of sternite V; vulva not extending beyond sternite V ..... *Aparapotamon huiliense* Dai & Chen, 1985 [China]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Potamiscus*: Species

The following key is modified from Dai (1999).

1 External orbital angle with indistinct teeth; gonopod I apex reaching to or slightly beyond abdominal lock tubercle 2

1′ External orbital angle with 9 or10 distinct teeth; gonopod I apex not reaching abdominal lock tubercle ..... *Potamiscus loshingensis* (Wu, 1934) [China]

2(1) External orbital angle with numerous, small teeth; anterolateral margin with 12−15 teeth; gonopod I with subdistal article length 1.6x distal article ..... *Potamiscus elaphrius* Dai, Chen, Liu, Luo, Yi, Liu, Gu, & Liu, 1990 [China]

2′ External orbital angle with few small teeth; anterolateral margin with 14−17 teeth; gonopod I with subdistal article length 1.9x distal article ..... *Potamiscus rongjingensis* Dai, Chen, Liu, Luo, Yi, Liu, Gu, & Liu, 1990 [China]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Tenuilapotamon*: Species

The following key is modified from Dai (1999).

1 Carapace anterolateral margin with numerous indistinct tubercles; maxilliped III merus distinctly broader than long (length-to-width ratio ca. 0.8); gonopod I with subdistal article length 2.0x distal article ..... *Tenuilapotamon joshuiense* (Dai, Song, He, Cao, Xu, & Zhong, 1975) [China]

1′ Carapace anterolateral margin with 16 or 17 small teeth; maxilliped III merus distinctly longer than broad (length-to-width ratio ca. 1.3); gonopod I with subdistal article length 2.2x distal article ..... *Tenuilapotamon latilum* (Chen, 1980) [China]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Geothelphusa*: *S*pecies

1 Gonopod I distally cylindrical or funicular, not simply acute 2

1′ Gonopod I distally acute ..... *Geothelphusa exigua* Suzuki & Tsuda, 1994 [Japan]

2(1) Gonopod I distally cylindrical..... 3

2′ Gonopod I distally funicular 4

3(2) Gonopod I slightly sinuous, almost straight, cylindrical distal end directed anteromedially ..... *Geothelphusa marmorata* Suzuki & Okano, 2000 [Japan (Yakushima Island)]

3′ Gonopod I strongly curved laterally, cylindrical distal end directed anterolaterally ..... *Geothelphusa mishima* Suzuki & Kawai, 2011 [Japan (Kuchierabu, Kuroshima, and Uji islands)]

4(2) Gonopod I slightly sinuous, funicular distal end directed anteromedially ..... *Geothelphusa dehaani* (White, 1847) [Japan]

4′ Gonopod I strongly curved laterally, funicular distal end directed anteriorly ..... *Geothelphusa koshikiensis* Suzuki & Kawai, 2011 [Japan (Kami-Koshiki and Shimo-Koshiki Islands]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Sinopotamon*: Species

The following key is modified from Dai (1999).

1 Carapace relatively flat 2

1′ Carapace distinctly convex 7

2(1) Maxilliped III merus with distinct medial depression 3

2′ Maxilliped III merus with indistinct medial depression 5

3(2) External orbital angle with distinct tubercles; epibranchial tooth with less than 20 tubercles; maxilliped III exopod reaching slightly beyond posterior merus margin 4

3′ External orbital angle with indistinct tubercle; epibranchial tooth with 20–22 small tubercles; maxilliped III exopod reaching ~½ length merus lateral margin ..... *Sinopotamon cochlearidigitum* Dai, Chen, Zhang, & Lin, 1986 [China]

4(3) External orbital angle with 4 or 5 distinct, round tubercles; epibranchial tooth with 13–16 round tubercles ..... *Sinopotamon yichangense* Dai, 1999 [China]

4′ External orbital angle with 8 or 9 distinct, flattened tubercles; epibranchial tooth with 18 or 19 small, flattened tubercles ..... *Sinopotamon yaanense* (Chung & Tsao, 1962) [China]

5(2) External orbital angle with 6 or 7 tubercles; epibranchial tooth with 18–20 tubercles; maxilliped III exopod reaching slightly beyond merus posterior margin 6

5′ External orbital angle without tubercle; epibranchial tooth with 18–20 small tubercles; maxilliped III exopod reaching ~½ length merus lateral margin ..... *Sinopotamon introdigitum* Dai, Chen, Zhang, & Lin, 1986 [China]

6(5) Gonopod I subdistal article length 2.2x distal article ..... *Sinopotamon chishuiense* Dai & Yuan, 1988 [China]

6′ Gonopod I subdistal article length 2.7x distal artcile ..... *Sinopotamon pingshanense* Dai & Liu, 1994 [China]

7(1) Maxilliped III merus with distinct medial depression 8

7′ Maxilliped III merus with indistinct medial depression 10

8(7) External orbital angle with indistinct tubercles; epibranchial tooth with or without tubercles 9

8′ External orbital angle with 4–7 distinct tubercles; epibranchial tooth with 20–24 tubercles ..... *Sinpotamon fuxingense* Dai & Liu, 1994 [China]

9(8) Epibranchial tooth without tubercle; gonopod I with subdistal article length 2.6x distal article ..... *Sinopotamon weiyuanense* Dai, Chen, Liu, Luo, Yi, Liu, Gu, & Liu, 1990 [China]

9′ Epibranchial tooth with 20–27 rounded tubercles; gonopod I with subdistal article length 2.3–2.4x distal article ..... *Sinopotamon davidi* (Rathbun, 1904) [China]

10(7) External orbital angle with tubercles; epibranchial tooth with numerous tubercles 11

10′ External orbital angle without tubercle; epibranchial tooth with 20–25 tubercles ..... *Sinopotamon ebianense* Huang, Luo, & Liu, 1986 [China]

11(10) External orbital angle with 6 very small tubercles; epibranchial tooth with 28–30 small tubercles; gonopod I with distal article comparatively broad, convex, not compressed ..... *Sinopotamon emeiense* Dai, 1990 [China]

11′ External orbital angle with 5 or 6 tubercles; epibranchial tooth with 12–14 tubercles; gonopod I with distal article stout, compressed distally ..... *Sinopotamon kwanhsiense* Tai & Sung, 1975 [China]

Malacostraca: Decapoda: Brachyura: Potamidae: Potamiscinae: *Longpotamon*: Species

All species here were transferred from *Sinopotamon* by Shih et al. (2016b) who did not provide a key. The following key is modified from Dai's (1999) key to *Sinopotamon* species.

1 Carapace relatively flat, physiognomy low 2

1′ Carapace slightly convex to convex, physiognomy relatively high 13

2(1) Maxilliped III merus with medial depression obscure or absent 3

2′ Maxilliped III merus with distinct medial depression 7

3(2) Maxilliped III merus with medial depression obscure; gonopod I distal article directed dorsally 4

3′ Maxilliped III merus without medial depression; gonopod I distal article directed medially, subdistal article length 3.3x distal article ..... *Longpotamon shensiense* (Rathbun, 1904) [China]

4(3) External orbital angle with large, rounded tubercles; gonodpod I subdistal article length ≥3.0x distal article 5

4′ External orbital angle with numerous small, rounded tubercles; gonopod I subdistal article length 3.0x distal article ..... *Longpotamon wushanense* (Dai, Chen, Liu, Luo, Yi, Liu, Gu, & Liu, 1990) [China]

5(4) External orbital angle with 5−7 tubercles; epibranchial tooth with 14−18 acute teeth or rounded tubercles; gonopod I subdistal article length 3.0−3.5x distal article 6

5′ External orbital angle with 9 or 10 small tubercles; epibranchial tooth with 16−22 acute teeth; gonopod I subdistal article length 3.9x distal article ..... *Longpotamon nanum* (Dai, Chen, Liu, Luo, Yi, Liu, Gu, & Liu, 1990) [China]

6(5) External orbital angle with 5 or 6 tubercles; epibranchial tooth with 14 or 15 rounded tubercles; gonopod I subdistal article length 3.0−3.5x distal article ..... *Longpotamon jichiense* (Du, Lai, Deng, & Shen, 1978) [China]

6′ External orbital angle with 6 or 7 tubercles; epibranchial tooth with 15−18 acute teeth; gonopod I subdistal article length 3.2x distal article ..... *Longpotamon depressum* (Dai, Chen, Song, Fan, Lin, & Zeng, 1979) [China]

7(2) Gonopod I distal article directed medially 8

7′ Gonopod I distal article directed dorsally 9

8(7) External orbital angle without tubercle; epibranchial tooth with 11−13 small teeth; gonopod I subdistal article length 3.4x distal article ..... *Longpotamon xiuningense* (Dai, 1999) [China]

8′ External orbital angle with 3 or 4 tubercles; epibranchial tooth with 6 or 7 sparse teeth; gonopod I subdistal article length >4.5x distal article ..... *Longpotamon yixianense* (Du, Lai, Deng, Shen, & Chen, 1981) [China]

9(7) External orbital angle with numerous small teeth 10

9′ External orbital angle with fewer than 10 tubercles 11

10(9) Epibranchial tooth with 12−15 sparse, acute teeth; gonopod I subdistal article length 3.8x distal article; gonopod I apex reaching slightly beyond suture between sternites V and VI ..... *Longpotamon anhuiense* (Dai & Fan, in Dai, Chen, Song, Fan, Lin, & Zeng, 1979) [China]

10′ Epibranchial tooth with 13 small teeth; gonopod I subdistal article length 2.6x distal article; gonopod I apex not reaching beyond suture between sternites V and VI ..... *Longpotamon acutum* (Dai, 1997) [China]

11(9) External orbital angle with 5 or 6 tubercles; epibranchial tooth with numerous teeth; gonopod I subdistal article length <3.0x distal article 12

11′ External orbital angle with 6 or 7 tubercles; epibranchial tooth with 15−18 tubercles; gonopod I subdistal article length 3.0x distal article ..... *Longpotamon tongshanense* (Dai, 1999) [China]

12(11) Epibranchial tooth with 12−15 teeth; gonopod I subdistal article length 2.4x distal article ..... *Longpotamon obliquum* (Dai, 1990) [China]

12′ Epibranchial tooth with 14−16 small teeth; gonopod I subdistal article length 2.8x distal article ..... *Longpotamon styxum* (Dai, 1990) [China]

13(1) Carapace slightly convex 14

13′ Carapace distinctly convex 28

14(13) Maxilliped III merus with medial depression obscure or absent 15

14′ Maxilliped III merus with medial depression distinct 21

15(14) Maxilliped III merus with medial depression absent 16

15′ Maxilliped III merus with medial depression obscure 18

16(15) External orbital angle with numerous small teeth; epibranchial tooth with at least 16 small teeth; gonopod I distal article directed laterally, subdistal article length <5.0x distal article 17

16′ External orbital angle with 4−6 tubercles; epibranchial tooth with 16−18 small teeth; gonopod I distal article directed dorsally, subdistal article length 5.0x distal article ..... *Longpotamon teritisum* (Dai, Chen, Zhang, & Lin, 1986) [China]

17(16) Epibranchial tooth with at least 16 small teeth ..... *Longpotamon denticulatum* (H. Milne Edwards, 1853) [China]

17′ Epibranchial tooth with 16−22 small teeth ..... *Longpotamon quadratapodum* (Dai, Chen, Zhang, & Lin, 1986) [China]

18(15) External orbital angle with or without tubercles/teeth; gonopod I distal article directed laterally or dorsally 19

18′ External orbital angle with numerous small tubercles; gonopod I distal article directed medially 20

19(18) External orbital angle without tubercle; epibranchial tooth with 15−18 tubercles; gonopod I distal article directed dorsally, subdistal article length 3.0−3.4x distal article ..... *Longpotamon decrescentum* (Dai, Chen, Zhang, & Lin, 1986) [China]

19′ External orbital angle with five small teeth; epibranchial tooth with 17 or 18 small teeth; gonopod I distal article directed laterally, subdistal article length 3.3x distal article ..... *Longpotamon hanyangense* (Dai, 1995) [China]

20(18) Epibranchial tooth with 18−20 tubercles; gonopod I subdistal article length 3.4x distal article ..... *Longpotamon cladopodum* (Dai, Chen, Zhang, & Lin, 1986) [China]

20′ Epibranchial tooth with 18−24 tubercles; gonopod I subdistal article length 2.8−3.0x distal article ..... *Longpotamon xingshanense* (Dai, Chen, Zhang, & Lin, 1986) [China]

21(14) Gonopod I distal article directed medially or laterally 22

21′ Gonopod I distal article directed dorsally, subdistal article length 3.1x distal article; external orbital angle with numerous unequal, rounded tubercles; epibranchial tooth with 15−17 indistinct tubercles ..... *Longpotamon changanense* (Dai, 1999) [China]

22(21) Gonopod I terminal article directed medially 23

22′ Gonopod I terminal article directed laterally 24

23(22) External orbital angle with 3 or 4 small teeth; epibranchial tooth with 9−14 small, widely spaced teeth; gonopod I distal article distinctly curved medially ..... *Longpotamon shanxianense* (Dai & Chen, 1981) [China]

23′ External orbital angle with 5 or 6 teeth; epibranchial tooth with 9−13 widely spaced teeth; gonopod I distal article slightly curved medially ..... *Longpotamon tongbaiense* (Dai & Chen, 1981) [China]

24(22) External orbital angle with 4−6 tubercles; epibranchial tooth with numerous tubercles; gonopod I subdistal article length ≥2.4x distal article 25

24′ External orbital angle without tubercle; epibranchial tooth with 15 or 16 tubercles; gonopod I subdistal article length 3.1x distal article ..... *Longpotamon tinghsiangense* (Bott, 1967) [China]

25(24) External orbital angle with 4 or 5 tubercles; epibranchial tooth with <17 tubercles; gonopod I subdistal article length <4.3x distal article 26

25′ External orbital angle with 4−6 tubercles; epibranchial tooth with 17−19 teeth; gonopod I subdistal article length ≥3.4x distal article ..... *Longpotamon shangchengense* (Dai, 1999) [China]

26(25) Male abdominal somite VI length-to-width ratio 2.0; epibranchial tooth with ≤15 distinct teeth; gonopod I subdistal article length 2.4x distal article 27

26′ Male abdominal somite VI length to width ratio 2.2; epibranchial tooth with 11−16 tubercles; gonopod I subdistal article length 4.3x distal article ..... *Longpotamon yangtsekiense* (Bott, 1967) [China]

27(26) Epibranchial tooth with 14 or 15 distinct teeth; gonopod I apex a single lobe ..... *Longpotamon jiangxianense* (Dai, 1999) [China]

27′ Epibranchial tooth with 13−15 narrow teeth; gonopod I apex bilobed ..... *Longpotamon chengkuense* (Huang, Luo, & Liu, 1986) [China]

28(13) Maxilliped III merus with medial depression obscure or absent 29

28′ Maxilliped III merus with medial depression distinct 32

29(28) External orbital angle with several tubercles/teeth; gonopod I distal article directed dorsally or medially 30

29′ External orbital angle with 2−5 small teeth; gonopod I distal article directed laterally, subdistal article length 4.2x distal article ..... *Longpotamon lansi* (Doflein, 1902) [China]

30(29) Gonopod I distal article directed dorsally 31

30′ Gonopod I distal article directed medially, subdistal article length 3.0−3.5x distal article; external orbital angle with 3−5 small teeth; epibranchial tooth with 15−17 teeth ..... *Longpotamon planum* (Dai, 1992) [China]

31(30) External orbital angle with numerous flattened tubercles; epibranchial tooth with 28−30 small tubercles; gonopod I subdistal article length 3.2x distal article ..... *Longpotamon turgidum* (Dai, Chen, Zhang & Lin, 1986) [China]

31′ External orbital angle with 2−4 acute teeth; epibranchial tooth with 10−12 acute teeth; gonopod I subdistal article length 2.7x distal article ..... *Longpotamon honanense* (Dai, Song, He, Cao, Xu, & Zhong, 1975) [China]

32(28) External orbital angle with 4−6 tubercles; epibranchial tooth with 7−15 teeth; gonopod I distal article directed dorsally 33

32′ External orbital angle with 3−5 tubercles; epibranchial tooth with 4 or 5 tubercles; gonopod I distal article directed laterally ..... *Longpotamon yueyangense* (Dai, 1995) [China]

33(32) External orbital angle with 4−6 small, rounded tubercles; epibranchial tooth with 14 or15 serrated teeth; gonopod I subdistal article length 4.2x distal article ..... *Longpotamon convexum* (Dai, 1995) [China]

33′ External orbital angle with 5 or 6 tubercles; epibranchial tooth with 7 or 8 widely spaced teeth; gonopod I subdistal article length 3.0x distal article ..... *Longpotamon exiguum* (Dai, 1997) [China]

Crustacea: Malacostraca: Caridea: Families

1 Pereopods I and II with chelae lacking elongated apical setal tufts (Fig. 16.6.16 D) 2

1′ Pereopods I and II with chelae bearing elongated apical setal tufts, forming sieving or scraping apparatus (Fig. 16.6.16 E) ..... **Atyidae [p. 877]**

2(1) Carapace lacking longitudinal sutures; antenna I dorsal flagellum with rami fused basally ..... **Palaemonidae [p. 879]**

2′ Carapace bearing single pair of straight, longitudinal, dorsolateral sutures; cavernicolous ..... Typhlocaridae, one genus: *Typhlocaris* [Mediterranean Basin]

Crustacea: Malacostraca: Caridea: Atyidae: Genera

1 Supraorbital spines absent; pereopods without exopod; diaresis variable 2

1′ Supraorbital spines present; pereopod with exopods present or absent; diaresis bearing one or two distal spinulae 6

2(1) Diaresis with numerous spines; troglobitic or not 3

2′ Diaresis bearing one or two distal spinulae; troglobitic ..... ***Typhlatya* [p. 877]**

3(2) Nine pairs of branchiae; pereopod I with arthrobranch 4

3′ Eight pairs of branchiae; pereopod I without arthrobranch; anchialne habitats; rostrum reduced, inerm; eyes rudimentary, lacking corneal facets or pigment ..... *Puteonator iraqiensis* Gurney, 1987 [Iraq]

4(3) Maxiliped II podobranch with lobed margins; male pereopod II and IV never distally dilated 5

4′ Maxiliped II podobranch with entire margins; male pereopod II and IV distally dilated ..... *Sinodina* [Oriental Region, may occur in southern Palaearctic China]

5(4) Male pleopod I endopod elongate oval to lanceolate; pleopod II appendix masculine width <2.0x appendix interna ..... ***Caridina* [p. 878]**

5′ Male pleopod I endopod suboval, length ≤2.0x width; pleopod II appendix masculine width >2.0x appendix interna ..... *Neocaridina* [Taxonomy confused. China, Japan, Korea, *Neocaridina davidi* Bouvier, 1904 invasive in Germany and Japan. Oriental]

6(1) Carapace pterygostomian spine absent; eyes functional or not 7

6′ Carapace pterygostomian spine present; pereopods with exopods present; eyes developed and functional ..... ***Dugastella* [p. 878]**

7(6) Eyes reduced, pigment absent; maxilliped III with arthrobranch; pereopods I−III with exopods; troglobitic 8

7′ Eyes developed, pigmented; maxilliped III arthrobranch absent; pereopods I and II bearing exopods ..... *Atyaephra* [Taxonomy somewhat confused, possible cryptic species. Europe, Lebanon, Morocco, Syria]

8(7) Male pleopod II appendix masculina longer than appendix interna, bearing spines or setae shorter than appendix masculina diameter ..... ***Troglocaris*** **[p. 878]**

8′ Male pleopod II with cylindrical appendix masculina, distal half with straight spines longer than appendix masculina diameter, and slightly longer than appendix interna ..... *Gallocaris inermis* (Fage, 1937) [France]

Crustacea: Malacostraca: Caridea: Atyidae: *Typhlatya*: Species

1 Rostrum shorter than reduced eye stalks; pereopod V dactylus with row of 36 slender marginal spines ..... *Typhlatya miravetensis* Sanz & Platvoet, 1995 [Spain]

1′ Rostrum length subequal to reduced eye stalks; pereopod V dactylus with row of 19−28 stout marginal spines ..... *Typhlatya arfaea* Jaume & Bréhier, 2005 [France]

Crustacea: Malacostraca: Caridea: Atyidae: *Caridina*: Species

1 Eyes pigmented and functional; rostrum teeth, if present, obvious, subequally spaced in proximal half; surface water species 2

1′ Eyes reduced, lacking pigment; body without pigment; rostrum with few, minute, scattered teeth; cave species ..... *Caridina alba* Li & Li, 2010 [China; Hubei]

2(1) Rostrum with dorsal teeth 3

2′ Rostrum without teeth ..... *Caridina typus* H. Milne-Edwards, 1837 [Widespread in Indo-Pacific]

3(2) Rostrum length >scaphocerite; rostrum length >antenna II peduncle, apical 0.25−0.3 dorsally with 0−3 teeth 4

3′ Rostrum length subequal to or < scaphocerite; rostrum length subequal to or < antenna II peduncle, *or* if longer, then apical 0.25−0.3 dorsally with >5 teeth 5

4(3) Preanal carina with acute spine ..... *Caridina gracilirostris* de Man, 1892 [Widespread in Indo-Pacific]

4′ Preanal carina inerm ..... *Caridina nilotica* (Roux, 1833) [Egypt, Sudan. Afrotropical]

5(3) Pterygostomian angle angular to projecting 6

5′ Pterygostomian angle rounded 7

6(5) Rostrum length ∼0.3x antenna II peduncle, rostrum just reaching proximal portion of second peduncle article; rostrum length ∼0.5x scaphocerite length; rostrum with 2−6 ventral teeth ..... *Caridina babaultioides* Yü, 1938 [China, Korea. Oriental]

6′ Rostrum length subequal to antenna II peduncle; rostrum length ∼0.9x scaphocerite length; rostrum with 5−8 ventral teeth ..... *Caridina togoensis* Hilgendorf, 1893 [Chad, Egypt, Sudan. Afrotropical]

7(5) Rostrum length ∼0.5x antenna II peduncle; rostrum length ≤0.75x scaphocerite; rostral apex dorsally inerm 8

7′ Rostrum length slightly >antenna II peduncle; rostrum length subequal to or slightly shorter than scaphocerite; rostral apex dorsally with teeth ..... *Caridina serratirostris* de Man, 1892 [Widespread in Indo-Pacific]

8(7) Carapace posterior to orbit without rostral spines; east Asia 9

8′ Carapace posterior to orbit with 6−8 rostral spines ..... *Caridina babulti basrensis* Al-Adhub & Hamzah, 1987 [Iraq]

9(8) Rostrum length ∼0.5x scaphocerite; rostrum ventrally with 0 or 1 tooth or with ≥7 teeth 10

9′ Rostrum length ∼0.75x scaphocerite; rostrum with 2−5 ventral teeth; telson apex rounded ..... *Caridina weberi* de Man, 1892 [Widespread in Indo-Pacific]

10(9) Rostrum with 7−15 ventral teeth; telson apex triangular ..... *Caridina multidentata* Stimpson, 1860 [China, Japan. Oriental]

10′ Rostrum with 0 or 1 ventral tooth; telson apex rounded ..... *Caridina spinipoda* Liang, Hong, & Yang, 1990 [China]

Crustacea: Malacostraca: Caridea: Atyidae: *Dugastella*: Species

1 Rivers and springs in Morocco ..... *Dugastella marocana* Bouvier, 1912

1′ Springs in southern Spain ..... *Dugastella valentina* (Ferrer Galdino, 1924)

Crustacea: Malacostraca: Caridea: Atyidae: *Troglocaris*: Subgenera

1 Superorbital spine present 2

1′ Superorbital spine absent 3

2(1) Male pleopod I endopodite with appendix interna short, indistinct, distally subequal to or slightly longer than endopodite lamina; male pleopod II appendix masculina triangular, at least 7x wider than appendix interna ..... *Troglocaris* sensu stricto
[Dinaric and western Caucasian karst regions]

2′ Male pleopod I endopodite with appendix interna digitiform, elongate, projecting well beyond endopodite lamina; male pleopod II appendix masculina with parallel margins, width ~3x appendix interna ..... *Troglocaris* (*Troglocaridella*) *hercegovinensis* (Babić, 1922)
[Bosnia and Herzegovina, Montenegro]

3(1) From Balkans ..... *Troglocaris* (*Spelaeocaris*)
[Bosnia and Herzegovina, Croatia, Montenegro]

3′ From Causcus Mountains ..... *Troglocaris* (*Xiphocaridinella*)
[Georgia, Russia]

Crustacea: Malacostraca: Caridea: Palaemonidae: Genera

Recent revisions have sunk *Palaemonetes* and *Exopalaemon* into *Palaemon* De Grave & Ashelby, 2013. See González-Ortegón & Cuesta (2006), Tzomos & Koukouras (2015), González-Ortegón et al. (2015) for keys to European *Palaemon* taxa.

1 Branchiostegial spine present, hepatic spine absent; marine, brackish, and freshwater forms; at least 24 described species with invasive species in Europe, the Caspian and Aral Seas, however, some of the taxonomy is unclear, at least for taxa in Asia ..... *Palaemon*
[China, Iran, Iraq, Japan, Korea, Egypt, Europe, Sudan]

1′ Branchiostegial spine absent, hepatic spine present ..... ***Macrobrachium*** **[p. 879]**

Crustacea: Malacostraca: Caridea: Palaemonidae: *Macrobrachium*: Species

Many species are kept in the aquarium trade, and two species are widespread in aquaculture. Introductions of new species are expected, as well as new species discoveries from China.

1 Unpigmented, eyes nonfunctional, with unpigmented corneas; caves 2

1′ Pigmented, with functioning eyes; surface waters 3

2(1) Chela with dactylus and pollex length 1.5x palm; rostrum length 0.5x carapace length ..... *Macrobrachium lingyunense* Li, Cai, & Clarke, 2006
[China]

2′ Chela with dactylus and pollex length 2x palm; rostrum length 0.7x carapace length ..... *Macrobrachium elegantum* Pan, Hou, & Li, 2010
[China]

3(1) Rostrum with ≤6 ventral teeth 4

3′ Rostrum with 8–14 ventral teeth ..... *Macrobrachium rosenbergii* (de Man, 1879)
[Oceana, Oriental. Invasive in China, Iran, widely grown in aquaculture]

4(3) Carpus length ≥1.5x merus 5

4′ Carpus length subequal to merus 7

5(4) Rostrum length ~0.6–0.8x scaphocerite length; rostral teeth 12–17, with 3–4 on carapace posterior to orbit, plus 2–5 ventral teeth 6

5′ Rostrum length subequal to scaphocerite; rostral teeth 12–16, with 2–3 on carapace posterior to orbit, plus 2–3 ventral teeth ..... *Macrobrachium nipponense* (De Haan, 1849)
[China, Japan, Korea. Oriental. Invasive in Belarus, Iran, Iraq, Kazakhstan, Moldova, Russia, Uzbekistan, Caspian Sea]

6(5) Rostrum length ~0.55–0.66x carapace length; carapace, abdomen, and telson covered in microspinulae, which are most dense laterally ..... *Macrobrachium formosense* Spence Bate, 1868 [Japan]

6′ Rostrum length subequal to carapace length; carapace, abdomen, and telson without microspinulae ..... *Macrobrachium inflatum* Liang & Yan, 1985 [China]

7(4) Rostrum with <5 ventral teeth; Asia 8

7′ Rostrum with ≥5 ventral teeth, if fewer, then occurring in Europe 10

8(7) Rostrum with more than one tooth posterior to orbit; Asia 9

8′ Rostrum with one tooth posterior to orbit ..... *Macrobrachium niloticum* (Roux, 1833) [Egypt, Sudan. Afrotropical]

9(8) Male pereopod II chela with cutting edges bearing small teeth in proximal third of pollex; pereopod II with carpus length distinctly < chela palm ..... *Macrobrachium asperulum* (von Martens, 1868) [China]

9′ Male pereopod II chela with cutting edges lacking teeth; pereopod II with carpus length subequal to chela palm ..... *Macrobrachium edentatum* Liang & Yan, 1986 [China]

10(7) Rostrum with three to five teeth posterior to orbit ..... *Macrobrachium maculatum* Liang & Yan, 1980 [China]

10′ Rostrum with two or three teeth posterior to orbit ..... *Macrobrachium dayanum* (Henderson, 1893) [Oriental. Invasive in Germany]

Malacostraca: Decapoda: Astacidea

Modified from Hobbs (1974).

1 Pleopod I present in males, functioning as a gonopod, reduced or absent in females; maxilliped II and III, plus pereopods I–III, with podobranch (coxal gill) with laminae bilobed and plaited; maxilliped I lacking branchial filaments 2

1′ Pleopod I absent; podobranch laminae never bilobed and plaited; maxilliped I with branchial filaments ..... **Parastacidae [p. 880]**

2(1) Mature males with pleopod I bearing a distal shallow sperm groove, or pleopod I composed of two or more terminal rami; male with one or more pairs of ischia bearing conical hooks; females with or without annulus ventralis 3

2′ Pleopod I distally cylindrical; ischia without hooks; females lacking annulus ventralis ..... **Astacidae [p. 880]**

3(2) Male pereopods III, IV, or both with hooks on ischia; females with annulus ventralis ..... **Cambaridae [p. 881]**

3′ Male pereopods II and III with hooks on ischia; females without annulus ventralis ..... Cambaroididae, one genus; ***Cambaroides*** **[p. 881]**

Malacostraca: Decapoda: Astacidea: Parastacidae: *Cherax*: Species

1 Carapace with four obvious dorsal ridges, two extending posteriorly from rostrum posterior corners, two extending posteriorly from orbital spines; areola (area between branchiocardic grooves) length ≤3x width ..... *Cherax quadricarinatus* (von Martens, 1868) [Invasive in Slovenia. Isolated records in Germany, Great Britain, Israel, Italy, Netherlands. Common in aquaculture. Australia.]

1′ Carapace with two obvious dorsal ridges, extending posteriorly from the rostrum posterior corners; areola length >4x width ..... *Cherax destructor* Clark, 1936 [Invasive in Italy, Spain. Common in aquaculture. Australia]

Malacostraca: Decapoda: Astacidea: Astacidae: Genera

Identifications of the three endemic European genera should be made with great caution, as overlap occurs between them (Śmietana et al., 2006). The species and subspecies delimited for the three endemic genera also show substantial overlap, and there is evidence for cryptic species. Thus, the keys stop at genus level. It also should be noted that some European native crayfish taxa are protected under various laws.

1 Telson with transverse suture 2

1′ Telson without transverse suture ..... *Pacifastacus leniusculus leniusculus* (Dana, 1852) [Nearctic. Invasive in Europe]

2(1) Two pairs of postorbital ridges; pleopod I distal lobes unequal; pleopod II exopodite length subequal to endopodite; maxilliped III merus with one medial spine, occasionally also with distal spine 3

2′ Only one pair of postorbital ridges, or (rarely) with extremely reduced second pair; pleopod I distal lobes subequal; pleopod II exopodite length distinctly < endopodite; maxilliped III merus typically with medial spine row, rarely with one spine ..... *Austropotamobius* [Europe]

3(2) Abdominal somites II–IV with pleura bearing acute spines; pleopod II with ventral process (talon) ..... *Pontastacus*

3′ Abdominal somites II and III with pleura rounded or angular, lacking spines, somite IV with pleura bearing obscure spine or not; pleopod II without ventral process ..... *Astacus* [Europe, to Caspian Sea]

Malacostraca: Decapoda: Astacidea: Cambaridae: Genera

Two genera with five invasive species are reported from the Palaearctic. Due to their popularity as aquarium subjects and as aquaculture stock, more species may be found in the future.

1 Mature males with pleopod I terminating in two rounded lobes and spiniform structure; females with annulus ventralis movable, not fused anteriorly to sternum ..... ***Procambarus*** **[p. 880]**

1′ Mature males with pleopod I terminating in two triangular or elongate lobes; females with annulus ventralis fused anteriorly to sternum ..... ***Faxonius*** **[p. 881]**

Malacostraca: Decapoda: Astacidea: Cambaridae: *Procambarus*: Species

1 Chela with dactyl straight or slightly curved; branchiocardic grooves not meeting dorsally (areola present), sometimes very close together 2

1′ Chela with dactyl sinuate; branchiocardic grooves meeting dorsally (areola absent) ..... *Procambarus clarkii* (Girard, 1852) [Nearctic. Introduced and invasive in Europe, Cyprus, northern Africa, and elsewhere]

2(1) Chela dactyl with dorsal margin straight 3

2′ Chela dactyl with dorsal margin concave ..... *Procambarus acutus* (Girard, 1852) [Great Britain, Netherlands]

3(2) Males and females present in each population; annulus ventralis transverse, projecting anteriorly, with sigmoid sinus .... *Procambarus alleni* (Faxon, 1884) [France, Germany]

3′ Parthenogenic females only; annulus ventralis campanuliform, with sinuate sinus ..... *Procambarus virginalis* Lyko, 2017 [Appeared in aquarium trade ~1995. Invasive in Austria, Croatia, Czech Republic, Germany, Hungary, Italy, Netherlands, Slovakia, Sweden, Ukraine, Afrotopics. Spreading]

Malacostraca: Decapoda: Astacidea: Cambaridae: *Faxonius*: Species

1 Anterolateral portions of carapace smooth; male pleopod I with apices parallel or convergent; acumen (rostrum apical portion) length subequal or < rostrum width at distal spine pair 2

1′ Anterolateral portions of carapace with scattered denticles; male pleopod I with apices divergent; acumen (rostrum apical portion) length > rostrum width at distal spine pair ..... *Faxonius limosus* (Rafinesque, 1817) [Nearctic. Invasive in Europe]

2(1) Chelae with dactyl lacking proximal, arcuate emargination 3

2′ Chelae with dactyl bearing proximal, arcuate emargination, separated from remainder of cutting edge by large tubercle .... *Faxonius immunis* (Hagen, 1870) [France, Germany]

3(2) Scaphocerite distal spine length ~0.5x scaphocerite length; scaphocerite distomedial margin subangular .... *Faxonius juvenilis* (Hagen, 1870) [France]

3′ Scaphocerite distal spine length ~0.8x scaphocerite length; scaphocerite distomedial margin evenly curved .... *Faxonius virilis* (Hagen, 1870) *sensu lato* [Great Britain, Netherlands]

Malacostraca: Decapoda: Astacidea: Cambaroididae: *Cambaroides*: Species

1 Telson lateral spines paired 2

1′ Telson lateral spines single 3

2(1) Rostrum medial carina present or obscure, but reaching rostral apex ..... *Cambaroides similis* (Koelbel, 1892) [China, Korean Peninsula]

2′ Rostrum medial carina present, but not reaching rostral apex, stopping approximately ~0.25x rostrum length before apex ..... *Cambaroides wladiwostokiensis* Birstein & Vinogradov, 1934 [Russia]

3(1) Rostrum medial carina obscure, or if present, tapering before rostral apex 4

3′ Rostrum medial carina present, extending to rostral apex ..... *Cambaroides dauricus* (Pallas, 1772) [China, Mongolia, North Korea, Russia]

4(3) Rostrum lacking marginal spines; chelae with scattered setal tufts ..... *Cambaroides schrenckii* (Kessler, 1874) [China, Russia]

3′ Rostrum with pair of marginal spines; chelae punctate with punctae lacking setae ..... *Cambaroides japonicus* (De Haan, 1841 [in De Haan, 1833–1850]) [Japan]

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Malacostraca: Mysida and Stygiomysida

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INTRODUCTION

Mysids and stygiomysids are primarily marine shrimp-like crustaceans, with approximately 1200 species known globally (Ahyong et al., 2011). Only some 35 species are found in Palearctic nonmarine waters (Porter et al., 2008; Daneliya et al., 2012). The majority of this continental diversity occurs in the Ponto-Caspian Basin, where mysids are found in the lower and middle reaches of the Volga, Don, Dnieper, Danube, and other large rivers draining into the Caspian, Azov, and Black Seas, in the brackish water Caspian Sea, and in coastal lakes. Several of the Ponto-Caspian species have been introduced outside their native ranges and have thereafter spread across Central and East European river systems. A few species are found in fresh waters of the Mediterranean Basin, including caves and other subterranean waters, and a number of "glacial relict" *Mysis* spp. are present in postglacial North Eurasian lakes. Mysids and stygiomysids are benthopelagic, found above various bottom habitats during daytime and vertically migrating during night. They can constitute an important food source for benthic and pelagic fishes. They are predominantly omnivorous filter feeders and predators.

LIMITATIONS

The keys encompass continental species occurring in fresh waters and in the brackish, landlocked Caspian Sea. Marine species that occasionally enter brackish water estuaries and lagoons are not included, but those which can be encountered in freshwater lakes and lower reaches of rivers are considered here.

The Palearctic mysids and stygiomysids are relatively well studied and usually readily identified to species level. In some cases, such as the recently diagnosed sibling species of the circumboreal *Mysis relicta* group, and the East Mediterranean freshwater species of *Diamysis*, morphological differences are relatively subtle. As much as possible, the keys are based on characters found in both sexes. Nearly all taxa are mysids of subfamily Mysinae in the Mysidae, represented here by 11 genera. The exceptions are two stygiomysid species, both restricted to Southern Italy, i.e., *Spelaeomysis bottazzi* from Lepidomysidae and *Stygiomysis hydruntina* from Stygiomysidae.

TERMINOLOGY AND MORPHOLOGY

Continental Palearctic mysid and stygiomysid adults range in size from about 5 to 40 mm. Though superficially resembling shrimp, these animals possess a brood pouch in females (Fig. 16.6.66 C). Within this brood pouch the embryos develop and hatch into juveniles, already fully resembling adult specimens, lacking only secondary sexual characters. The adult male is recognized by the elongated **endopod** of **pleopod IV** (Mysida) and presence of **penes** (Fig. 16.6.66 B).

The body is composed of a **cephalothorax** (12 segments) and **abdomen** (6 segments and **telson**). The cephalothorax is covered by a **carapace**, which is fused with the anterior part of body and only leaves visible the last two to four thoracic segments (Figs. 16.6.66 and 68 A). The anterior margin of the carapace (as seen from dorsal view) is usually slightly produced (Figs. 16.6.67 B, 68, 73, 76 A, B, 77, 78, 82 C, D, and 88 A, B), and its shape is often diagnostic. Under this anterior margin, a small, often sharp, **subrostral plate** can be seen (Figs. 16.6.73, 82 C, D, 85 A, and 88 A, B). The cephalic part of the carapace is demarcated from thoracic part by lateral **pleurocervical fissures** in mysids (Figs. 16.6.82 C, D). Mysids have movable compound eyes, normally consisting of a proximal stalk and a distal cornea (Fig. 16.6.3 C), consisting of visual elements (ommatidia) (Figs. 16.6.68 A and 77 E), but in stygiomysids only broad ocular plates are present (Figs. 16.6.67 A, B).

Most appendages are biramous, consisting of an **endopod** and an **exopod**, which rest on a short **peduncle** (**protopod**). Antenna I has two flagellae, antenna II has one. At the base of antenna II, the flat, lamelliform **antennal scale** is a balance organ, whose shape and structure make important generic and specific diagnostic characters (Figs. 16.6.66, 68, 69, 73, 77 A, 79, 84, 85 A, 87, and 88 A, B). In stygiomysids, the antennal scale is rudimentary. In males the antenna I, peduncle article 3 bears a **sensory process** (Figs. 16.6.66 B, 68 C, and 86).

The mouthparts are relatively invariable. The flat upper lip (**labrum**), in a number of genera, has a strong apical spine. The **mandible** bears a **mandibular palp** of three articles (Figs. 16.6.66 B, 78 F, and 88 C), which often has useful diagnostic characters. **Maxilla II** in the Mysidae (Figs. 16.6.74, 78 E, 81 E, F, and 82 E) consists of a flat, setose, uniarticulate exopod, whose shape sometimes varies between species (Figs. 16.6.82 E, H); an endopod of two (rarely three) articles, with the second often bearing strong spiniform setae (Fig. 16.6.74 B) of different shape, size, and number (Figs. 16.6.78 D, E); and four strongly setose protopodal plates.

There are eight pairs of biramous thoracopods, of which one (in Lepidomysidae and Stygiomysidae) or two (Mysidae) are differentiated into **maxillipeds** and the remaining pairs are **pereopods**. All thoracopods in Mysidae have a multiarticulate, setose, swimming exopod (Fig. 16.6.66) and a more robust endopod of six articles, both with a strong basal article (Fig. 16.6.71 A). In stygiomysids the maxilliped exopod is rather small, laminar, and the endopod has five articles. The endopod is subdivided into a **preischium**, **ischium**, **merus**, **carpus**, **propodus,** and **dactylus**. In mysids, the carpus and propodus are fused (**carpopropodus**) and subdivided into a number of articles. **Maxilliped I** is slightly shorter than **maxilliped II**. In some genera the first two maxilliped I endopod articles also have setose medial endites, whose size is usually a generic marker. The mysid maxilliped II is a more slender structure, resembling pereopods (Figs. 16.6.78 B, C). The proportions of articles, dactylar and paradactylar setae shape, and even the position and length of thoracopod setae, are taxonomically important. In females, the last two (freshwater mysids), four (Stygiomysidae), or seven (Lepidomysidae) pereopods pairs have large basal plates (**oostegites**), which form the brood pouch (**marsupium**). In males, the last pereopod pair bears **penes** at the base (Fig. 16.6.66 B).

The mysid pleopods are mostly small monoramous plates, although pleopod II in males is usually biramous and the pleopod IV endopod is long, with two to five articles, and one or two distal **flagellae**, probably assisting in copulation (Figs. 16.6.66 B and 72). In *Hemimysis* sp., pleopod V is also biramous. In contrast, stygiomysids have all five pleopod pairs in both sexes biramous, with the exopod bearing two or three articles. The uropods are flat and biramous (Fig. 16.6.66). The uropod protopod of lepidomysids and stygiomysids has a ventral lobe or process, bearing strong spiniform setae (Figs. 16.6.67 C, D). The uropod exopod is generally of one article, margined with

long setae. Only in *Spelaeomysis* is the exopod of two articles, with the lateral margin of the basal article bearing strong, spiniform setae. In *Stygiomysis*, the exopod lateral margin is smooth, terminating in two spiniform setae. Both rami are margined by long setae. The uropod endopod of the Mysidae has a balance sensory organ (**statocyst**). Additionally, the uropod endopod in many mysids is armed with medial spiniform setae, and their position and number are taxonomically important (Fig. 16.6.75).

The mysid telson has a typical shape and structure for each genus (Figs. 16.6.66, 70, 76 C, D, 80, 81 A–D, 83 C, D, and 83 B, C). It can be linguiform, triangular, trapezoidal, posteriorly truncated, or cleft. The margins bear spiniform setae and sometimes also filiform setae. The apical margin or cleft is armed with short spinules of various number and shape.

MATERIAL PREPARATION AND PRESERVATION

Mysids can be preserved and further manipulated in ethanol. A genus level identification does not require any specimen preparation or large magnification optics, but species level identification typically requires the use of a compound microscope and prior dissection and mounting of appendages. Temporary slides can be made using glycerol or glycerol-gelatin. The best medium for permanent slides is Canada Balsam, which requires the specimens be dehydrated through an ethanol series. Alternative media for permanent slides are Faure–Berlese's fluid and Euparal.

KEYS TO MYSIDA AND STYGIOMYSIDA

Malacostraca: Mysida and Stygiomysida: Orders

(see also Malacostracan Order keys).

1	Eyes normally developed (with stalk and cornea) (Fig. 16.6.66) or without cornea (Fig. 16.6.68 A); uropodal endopod with statocyst (Fig. 16.6.67 E); uropodal protopod with no ventral medial lobe or process (Fig. 16.6.69 E) ..... Mysida, one family: **Mysidae [p. 885]**
1′	Eyes reduced to flat ocular plate with no visual elements (Figs. 16.6.67 A, B); uropodal endopod lacking statocyst (Figs. 16.6.67 C, D); uropodal protopod with a relatively short ventral medial lobe (Fig. 16.6.67 C) or a very long process (Fig. 16.6.67 D), bearing spiniform setae ..... **Stygiomysida [p. 888]**

Mysida: Mysidae: Genera

1	Eyes with cornea (Figs. 16.6.66, 68 B–D, 73, 76 A, B, 77, 79, 82 C, D, 85 A, 86, 88 A, B, and 89 A, B) 2
1′	Eyes without a cornea (Fig. 16.6.68 A); uropodal endopod with one proximal spiniform seta near statocyst (Fig. 16.6.67 E); telson trapezoid, with semilunar distal cleft; hypogean ..... *Troglomysis vjetrenicensis* Stammer, 1936 [Bosnia and Herzegovina]
2(1)	Antennal scale margin entirely setose (Figs. 16.6.58 B–D, 69 A–E, 77 A, and 79) 3
2′	Antennal scale lateral margin without setae at least in basal half (Figs. 16.6.69 F–J, 84, and 87) 7
3(2)	Telson either apically cleft, evenly truncated, smoothly rounded or triangular (Figs. 16.6.70 B–H, 76 C, D, and 80) 4
3′	Telson with a posterior linguiform plate extending between lateral terminal spiniform setae (Fig. 16.6.70 A); eyes stalk elongate, three to four times as long as cornea (Figs. 16.6.66 A and 68 B); antennal scale with distinct distal article (Fig. 16.6.69 A); marine, occasionally in fresh waters ..... *Mesopodopsis slabberi* van Beneden, 1861 [Sea of Azov, Black Sea, and Mediterranean Sea basins]
4(3)	Telson with an apical cleft (Figs. 16.6.74 B, E, H and 76 C, D) 5
4′	Telson without cleft, triangular (Figs. 16.6.70 F and 80 A) or trapezoidal (Fig. 16.6.80 B), apically truncated), antennal scale distally pointed, uropodal endopod with a dense, cristaform row of medial spiniform setae in proximal part (Fig. 16.6.75 G) ..... ***Neomysis* [p. 886]**
5(4)	Telson shorter than the last abdominal segment; antennal scale with a well-developed distal article (Figs. 16.6.69 D); pereopodal carpopropodus of two to four articles (Figs. 16.6.71 D, E) 6
5′	Telson longer than the last abdominal segment; antennal scale with rudimentary distal article (Fig. 16.6.69 E); pereopodal carpopropodus of 5 to 12 articles ..... ***Mysis* [p. 886]**
6(5)	Antennal scale distal article length 0.3–0.4× entire scale, in males the article is acute and slightly medially bent (Fig. 16.6.69 B), in females the article apex is rounded (Fig. 16.6.69 C); male pleopod IV exopod uniarticulate, mucronate, with three posterior spines and a short distal flagellum (Fig. 16.6.72 A) ..... *Limnomysis benedeni* Czerniavsky, 1882 [Ponto-Caspian Basin. Invasive elsewhere]

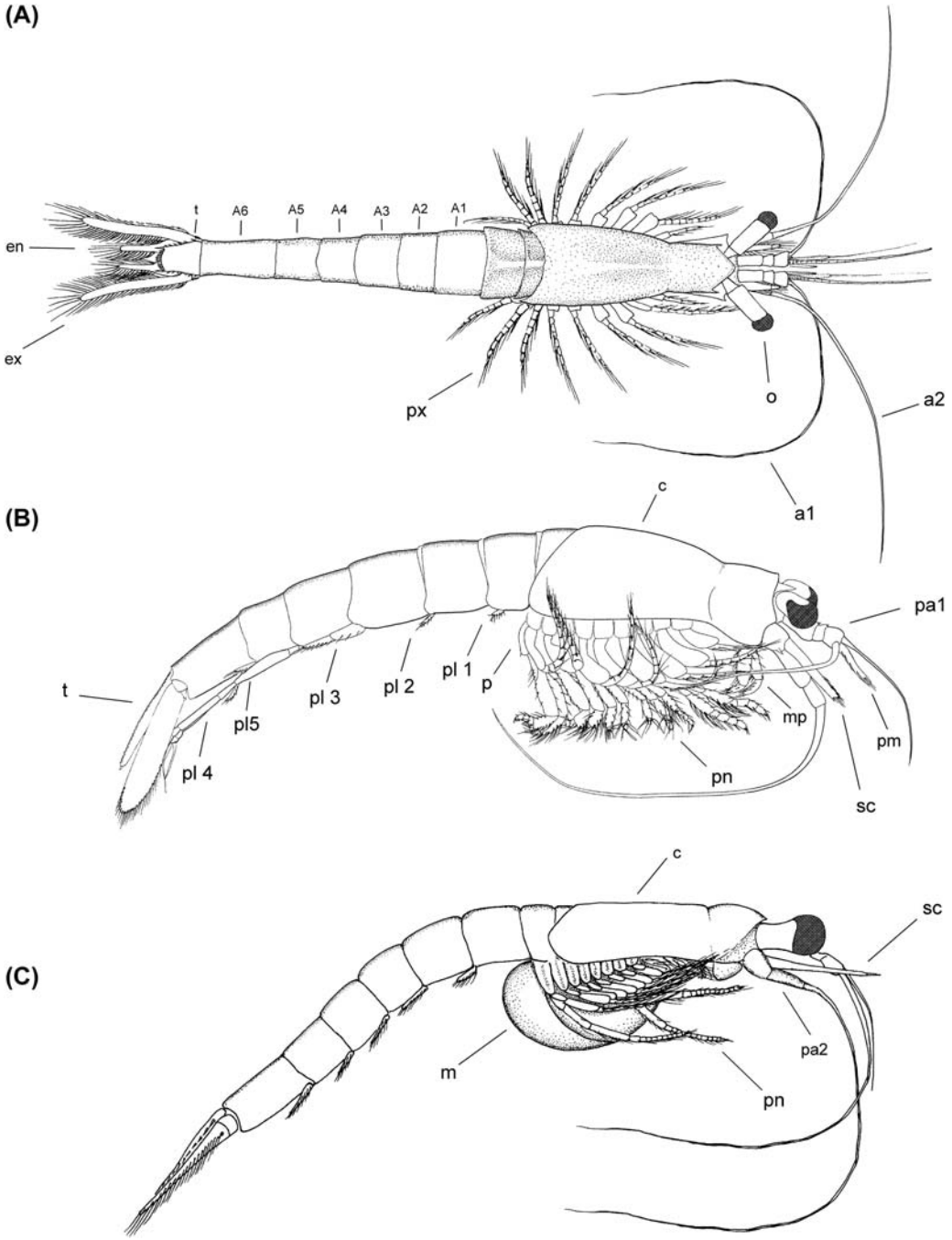


FIGURE 16.6.66 General habitus of mysids: (A) *Mesopodopsis slabberi*, dorsal view of male; (B) *Paramysis (Metamysis) inflata*, lateral view of male; (C) *Schistomysis elegans*, lateral view of female; *a1*, antenna I; *A1-A6*, abdominal segments; *a2*, antenna II; *c*, carapace; *en*, uropodal endopod; *ex*, uropodal exopod; *m*, marsupium; *o*, eye; *p*, penis; *pa1*, peduncle of antenna I; *pa2*, peduncle of antenna II; *pl1–pl5*, pleopods I–V; *pm*, processus masculinus; *pn*, pereopodal endopod; *px*, pereopodal exopod; *sc*, antennal scale; *t*, telson.

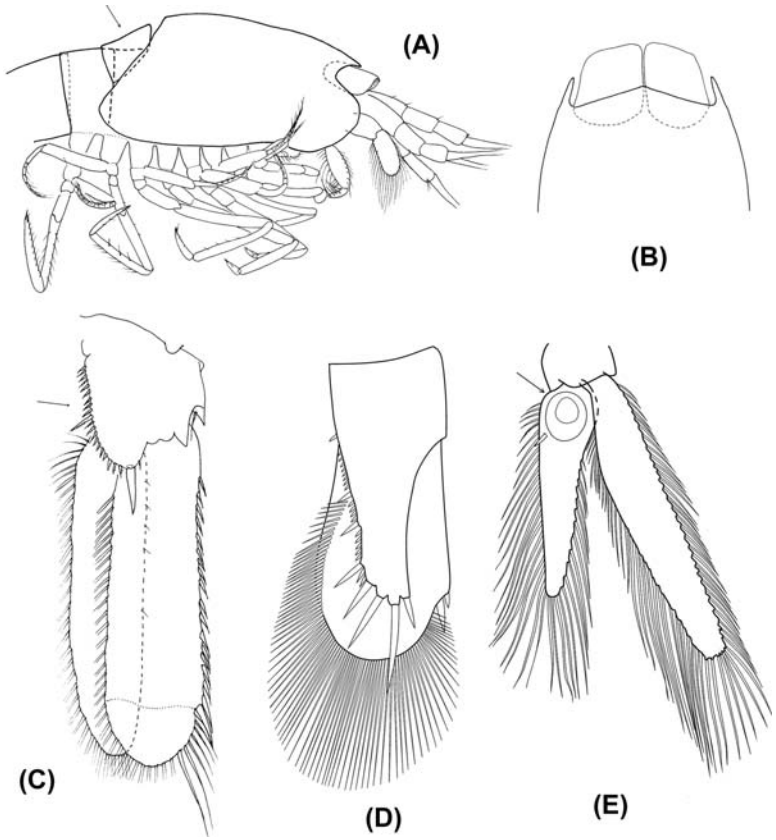


FIGURE 16.6.67 (A) *Spelaeomysis bottazzii*, anterior body part (cephalothorax), lateral view of male; *arrow* indicates dorsal scale; (B) *Spelaeomysis bottazzii*, head with eyes (appendages not shown), dorsal view; (C) *Spelaeomysis bottazzii*, uropod, ventral view; *arrow* indicates protopodal ventromedial lobe; (D) *Stygiomysis hydruntina*, uropod, ventral view; *arrow* indicates protopodal ventromedial process; (E) *Troglomysis vjetrenicensis*, uropod, ventral view; *arrow* indicates statocyst. *(D) From Caroli (1937), with modifications; (E) from Stammer (1936), with modifications.*

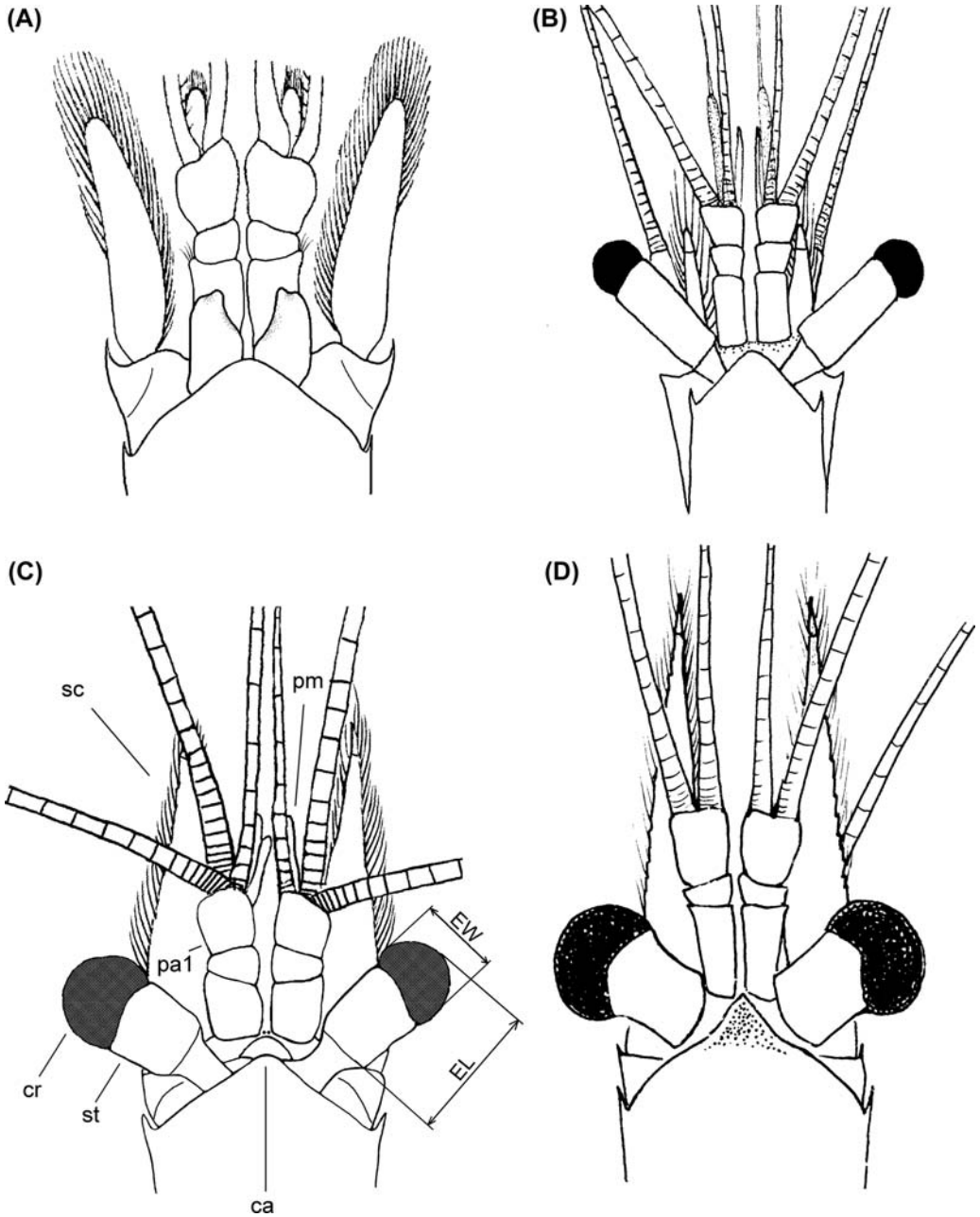


FIGURE 16.6.68 Head, dorsal view: (A) *Troglomysis vjetrenicensis*, male; (B) *Mesopodopsis slabberi*, male; (C) *Limnomysis benedeni*; *ca*, dorsal anterior margin of carapace; *cr*, eye cornea; *EL*, eye length; *EW*, eye width; *pa1*, peduncle of antenna I; *pm*, processus masculinus; *st*, eye stalk; (D) *Neomysis awatschensis*, female. *(A) From Stammer (1936), with modifications.*

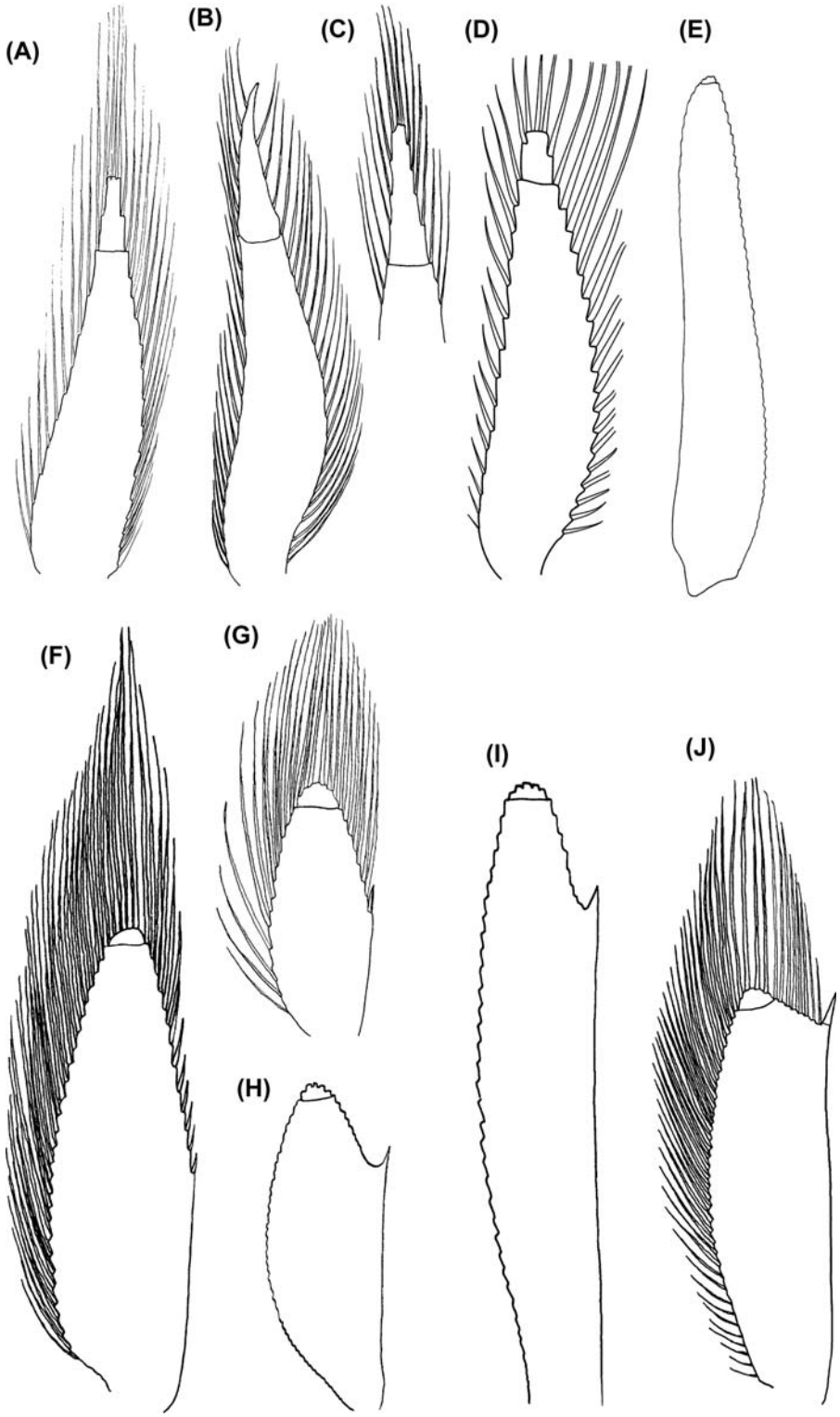


FIGURE 16.6.69 Antennal scales (exopod of antenna II): (A) *Mesopodopsis slabberi*; (B) *Limnomysis benedeni*, male; (C) *Limnomysis benedeni*, distal part, female; (D) *Diamysis pusilla* (from G.O. Sars, 1907, with modifications); (E) *Mysis microphthalma* (setae not shown); (F) *Hemimysis anomala*; (G) *Katamysis warpachowskyi*; (H) *Caspiomysis knipowitschi* (setae not shown); (I) *Schistomysis elegans* (setae not shown); (J) *Paramysis (Metamysis) ullskyi*.

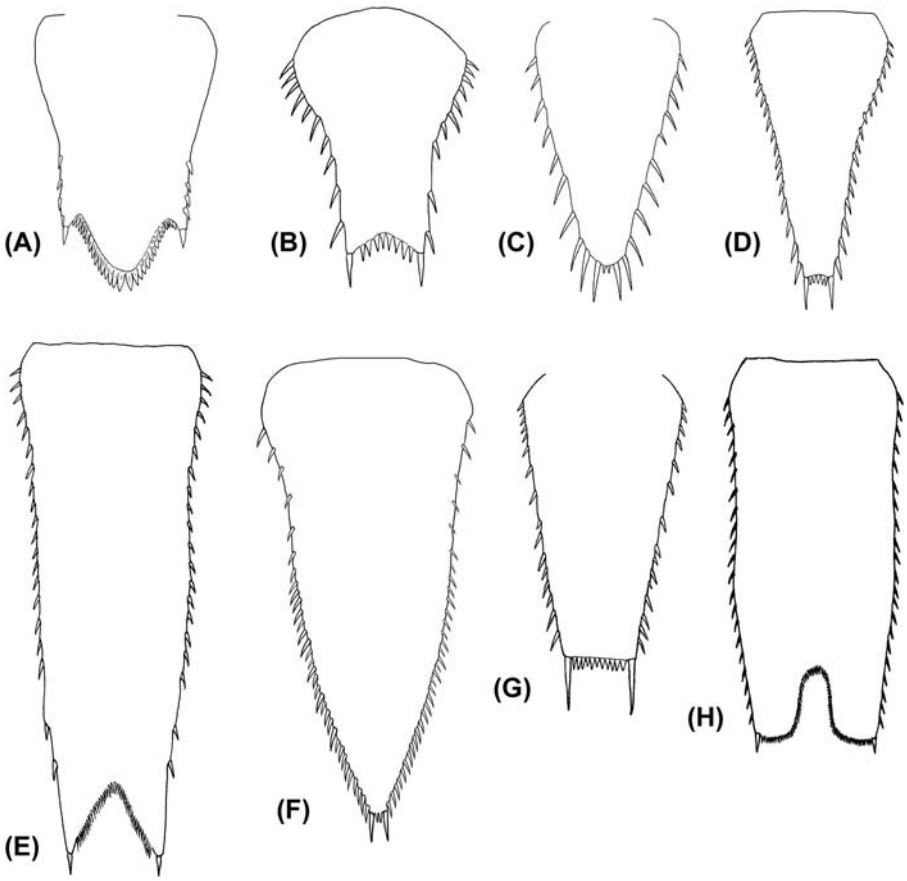


FIGURE 16.6.70 Telson: (A) *Mesopodopsis slabberi*; (B) *Limnomysis benedeni*; (C) *Katamysis warpachowskyi*; (D) *Caspiomysis knipowitschi*; (E) *Mysis caspia*; (F) *Neomysis japonica*; (G) *Hemimysis anomala*; (H) *Schistomysis elegans*. *(F) From Ii (1964), with modifications.*

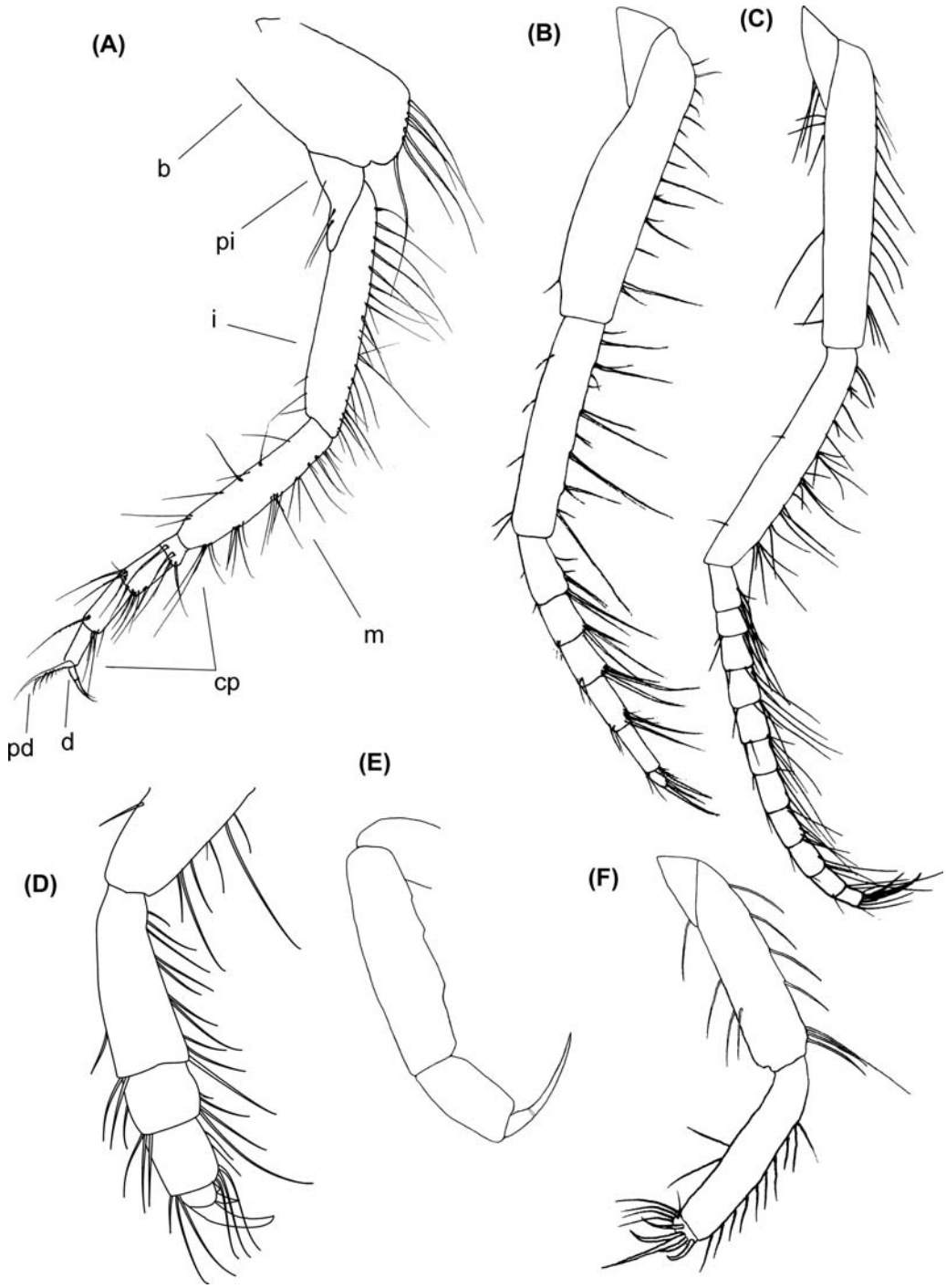


FIGURE 16.6.71 Pereopodal endopod: (A) *Caspiomysis knipowitschi*, pereopod IV; *b*, basis; *cp*, carpopropodus; *d*, dactylus; *i*, ischium; *m*, merus; *pd*, paradactylar seta; *pi*, preischium; (B) *Hemimysis anomala*, pereopod I; (C) *Schistomysis elegans*, pereopod I; (D) *Diamysis pusilla*, carpopropodus of pereopod I; (E) *Diamysis hebraica*, carpopropodus of pereopod I (setae not shown); (F) *Katamysis warpachowskyi*, pereopod VI. *(D) from G.O. Sars, 1907, with modifications; (E) from Almeida Prado-Por (1981) with modifications.*

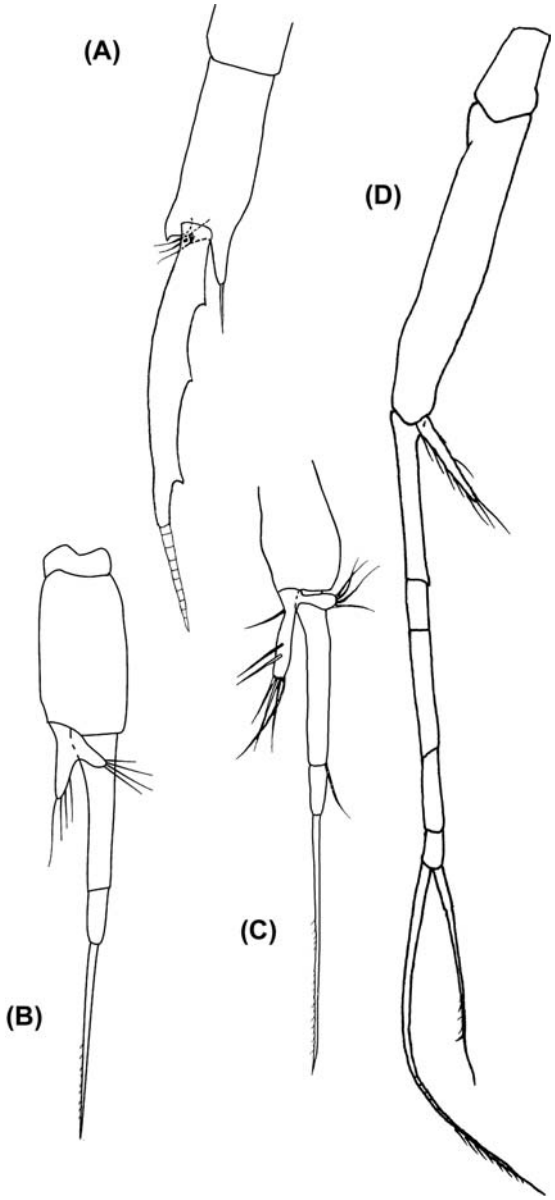


FIGURE 16.6.72 Pleopod IV of male: (A) *Limnomysis benedeni*; (B) *Diamysis pusilla*; (C) *Diamysis hebraica*; (D) *Mysis microphthalma*. *(A) From G.O. Sars (1907), with modifications; (C) from Almeida Prado-Por (1981) with modifications.*

6′ Antennal scale distal article only about 0.1 times the length of entire scale, with apex rounded in both sexes (Fig. 16.6.69 D); male pleopod IV exopod of two articles, cylindrical, with long distal seta (Figs. 16.6.72 B, C) ..... ***Diamysis*** **[p. 887]**

7(2) Telson distally cleft or evenly truncated, with distal margin bearing at least three small spinules (Figs. 16.6.70 D, G, H, 81 A–D, 83 C, D, and 84 B, C); pereopodal carpopropodus of 2–11 articles (Figs. 16.6.71 A–E, 82 A, B, 83 F, 85 D, E, 88 F–H, and 89 C) 8

7′ Telson linguiform, with only 1–2 apical small spinules (Fig. 16.6.69 C); pereopod III–VI carpopropodus reduced, of one article (Fig. 16.6.71 F); labrum with apical spine ..... *Katamysis warpachowskyi* G.O. Sars, 1893 [Ponto-Caspian. Invasive in eastern Europe]

8(7) Carapace anterior margin with a sharp triangular pseudorostral plate (Figs. 16.6.73 A, 82 C, D, 85 A, and 88 A, B); antennal scale lateral margin with strong terminal spiniform seta (Figs. 16.6.69 J, 84, and 87) 9

8′ Carapace anterior margin with rounded pseudorostral plate (Fig. 16.6.73 B); antennal scale lateral margin without strong spiniform seta, but bearing a line of robust setae, becoming longer distally (Fig. 16.6.69 F) ..... *Hemimysis anomala* G.O. Sars, 1907 [Ponto-Caspian. Invasive in central and northern Europe]

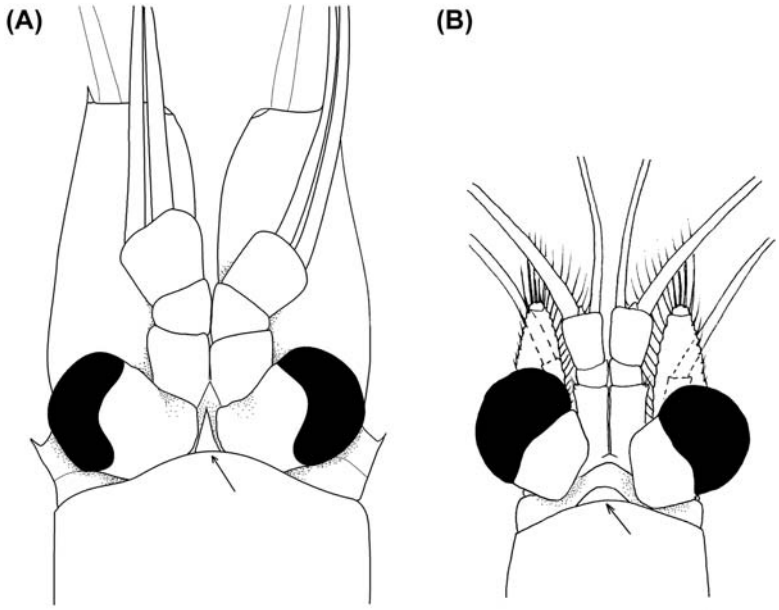


FIGURE 16.6.73 Head, dorsal view: (A) *Paramysis (Paramysis) eurylepis*, female; (B) *Hemimysis anomala*, female. *Arrow* indicates subrostral plate.

9(8) Pereopodal carpopropodus of 4 or 10 articles; maxilla II endopod with only setae (Fig. 16.6.81 F) or 1–3 additional small spiniform setae (Figs. 16.6.74 A, 81 E, and 82 E) 10

9′ Pereopods I–III, IV–VI carpopropodus of three articles; maxilla II endopod with more than 10 long distolateral spiniform setae (Fig. 16.6.74 B); telson triangular, apically evenly truncated, with 3–5 posterior spinules (Fig. 16.6.70 D) ..... *Caspiomysis knipowitschi* G. O. Sars, 1907 [Caspian Sea]

10(9) Uropodal endopod medially with a dense row of spiniform setae (Fig. 16.6.75 A); pereopodal carpopropodus of 10 or 11articles (Fig. 16.6.71 C); telson cleft (Fig. 16.6.70 H) ..... *Schistomysis elegans* G. O. Sars, 1907 [Caspian Sea]

10′ Uropodal endopod medially with separated spiniform setae (Figs. 16.6.75 B, C); pereopodal carpopropodus of four articles ..... ***Paramysis*** **[p. 887]**

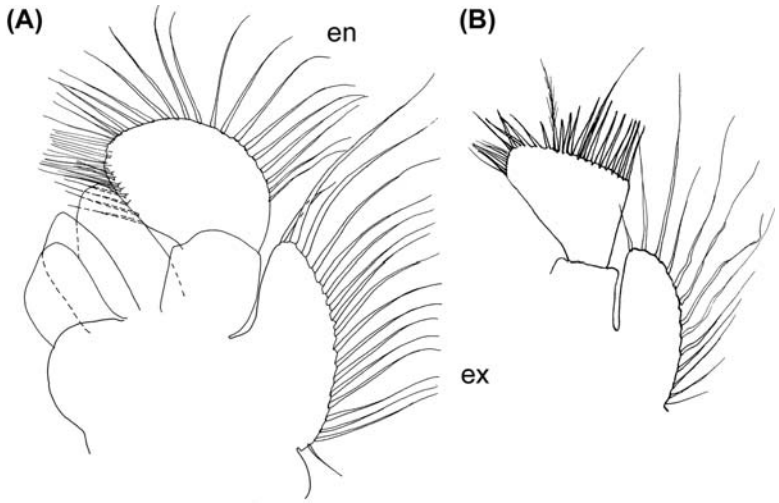


FIGURE 16.6.74 Maxilla II: (A) *Paramysis (Metamysis) grimmi*; *en*, endopod; *ex*, exopod; setae on endites (inner plates) not shown; (B) *Caspiomysis knipowitschi* (endites not shown).

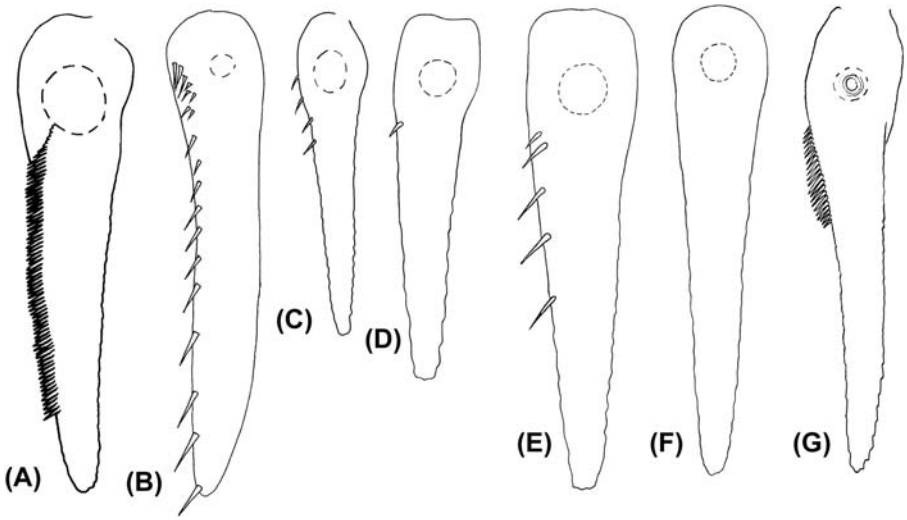


FIGURE 16.6.75 Uropodal endopods (setae not shown): (A) *Schistomysis elegans*; (B) *Paramysis (Metamysis) inflata*; (C) *P. (Nanoparamysis) loxolepis*; (D) *Mysis amblyops*; (E) *M. macrolepis*; (D) *M. microphthalma*.

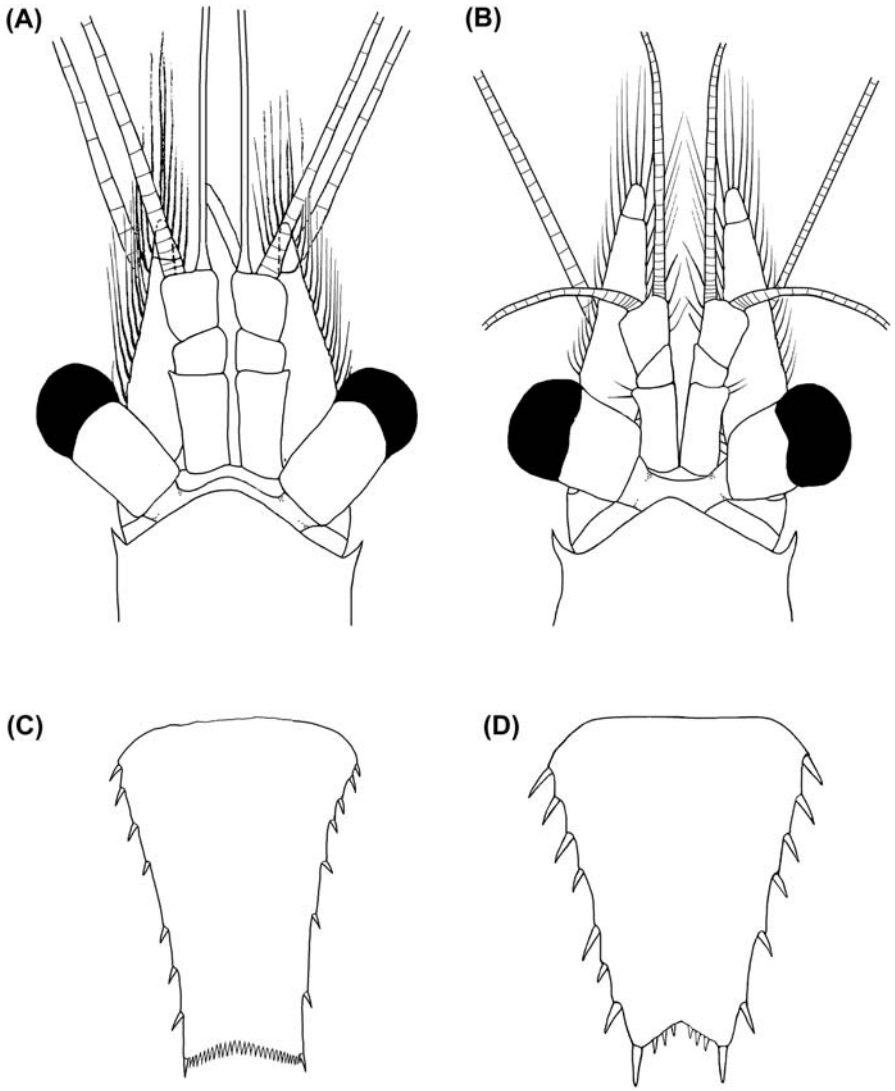


FIGURE 16.6.76 *Diamysis pengoi* (A and C) and *Diamysis pusilla*: (A) head of male, dorsal view; (B) head of female, dorsal view; (C and D) telson. *(B and D) from G.O. Sars (1907), with modifications.*

Mysida: Mysidae: *Neomysis*: Species

1 Carapace rostral plate narrowly triangular: sharp or apically rounded (Figs. 16.6.68 D and 79 A), pereopodal carpopropodus of 6–8 articles 2

1′ Carapace rostral plate broadly rounded (Fig. 16.6.79 B), pereopodal carpopropodus of 8–12 articles; telson triangular, distally strongly narrowed (Fig. 16.6.70 F) ..... *Neomysis japonica* Nakazawa, 1910 [China, Japan]

2(1) Telson triangular, distally strongly narrowed (Fig. 16.6.80 A), distal width 0.12–0.14 times proximal width ..... *Neomysis integer* Leach, 1814 [Europe]

2′ Telson weakly narrowed distally (Fig. 16.6.80 B), distal width 0.22–0.27 proximal width ..... *Neomysis awatschensis* Brandt, 1851 [North-West Pacific]

Mysida: Mysidae: *Mysis*: Species

1 Eyes large, cornea produced beyond carapace lateral sides; ratio between head region of carapace width and eye length 1.8–1.9 (Figs. 16.6.77 A, B) 2

1′ Eyes rather small, not produced or slightly produced beyond carapace lateral sides; ratio between head region of carapace width and eye length 2.5–3.3 (Figs. 16.6.77 C–E) 5

2(1) Antennal scale length 4–5.5× width, ~1.5× antenna I peduncle length; pereopodal carpopropodus of 5–8 articles 3

2′ Antennal scale length 7× width, <2× antenna I peduncle length; pereopodal carpopropodus of 8–12 articles ..... *Mysis caspia* G.O. Sars, 1895 [Caspian Sea]

3(2) Carapace dorsal posterior emargination shallow, <0.17 x total carapace length; female maxillipede II merus with setae longer than 0.6 x merus length (Fig. 16.6.78 C) 4

3′ Carapace posterior emargination rather deep, >0.17 (1/6) x total carapace length (Fig. 16.6.78 A); female maxillipede II merus distolateral setae > 0.6 x merus length (Fig. 16.6.78 B) ..... *Mysis relicta* Lovén, 1862 [Northern Europe, Baltic Sea]

4(3) Mandibular palp, palpomere 2 with 1–3 distolateral setae (Fig. 16.6.78 G); maxilla II endopod distally with an uneven row of serrated spiniform setae (two to six medial setae abruptly shorter than others) (Fig. 16.6.78 D) ..... *Mysis salemaai* Audzijonytė & Väinölä, 2005 [Northern Europe, Baltic Sea]

4′ Mandibular palp, palpomere 2 with 4–8 distolateral setae (Fig. 16.6.78 F); maxilla II endopod distally with a smooth row of serrated spiniform setae that gradually get shorter medially (Fig. 16.6.78 E) ..... *Mysis segerstralei* Audzijonytė & Väinölä, 2005 [Arctic-subarctic circumpolar]

5(1) Uropodal endopod with 1–5 spiniform setae (Figs. 16.6.75 D, E) 6

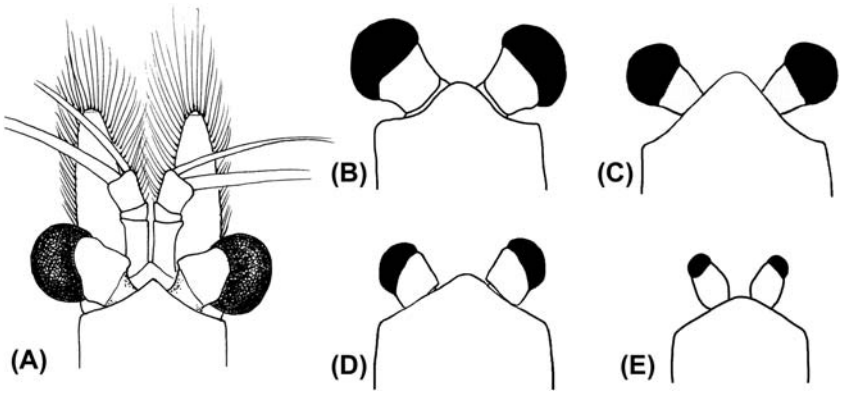


FIGURE 16.6.77 *Mysis* species: head (and anterior part of carapace); dorsal view: (A) *M. relicta*; (B) *M. caspia*; (C) *M. macrolepis*; (D) *M. microphthalma*; (E) *M. amblyops*.

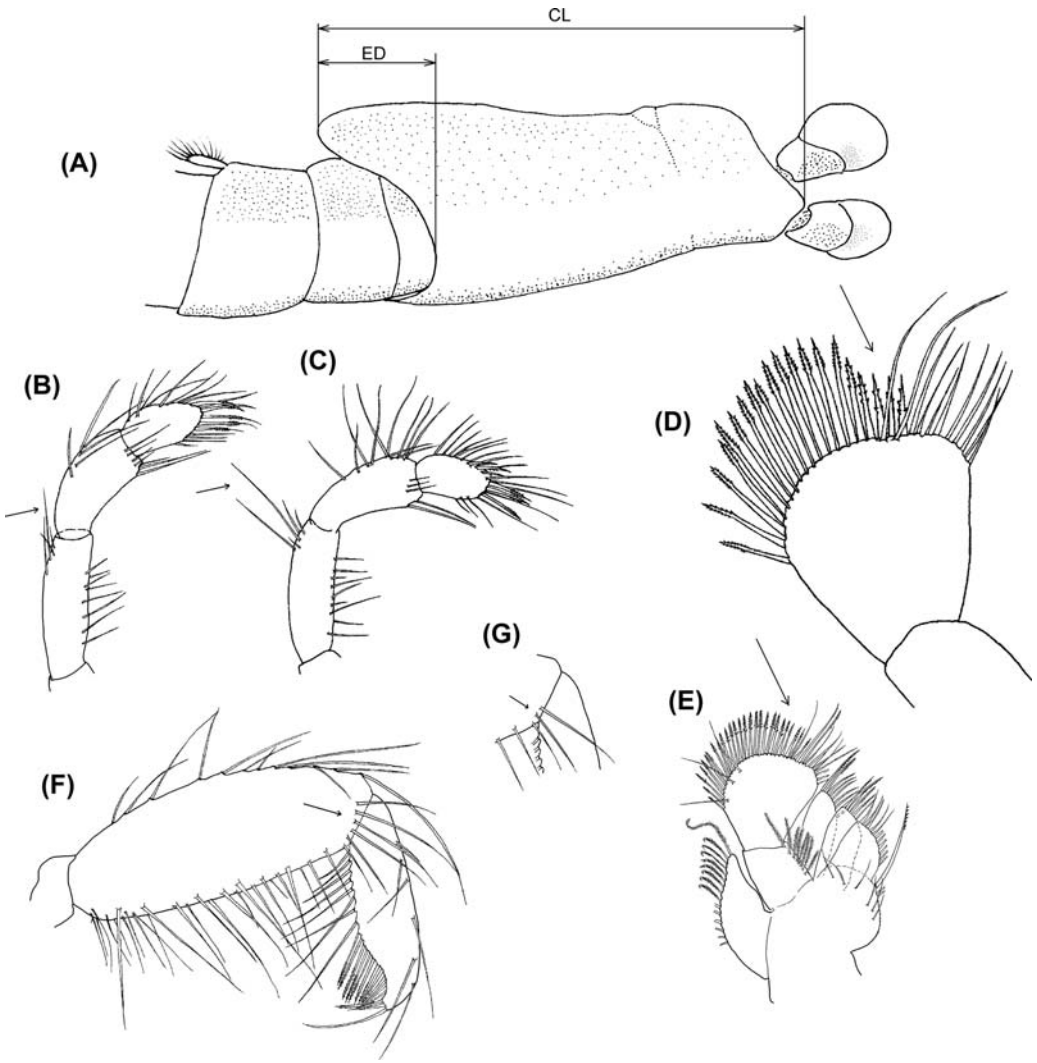


FIGURE 16.6.78 *Mysis* species: (A and B) *Mysis relicta*; (C, D, and G) *M. salemaai* (E and F) *M. segerstralei*. (A) carapace, dorsolateral view; measurements for the depth of posterior emargination: *CL*, total length of carapace; *ED*, depth of emargination; (C) maxilliped II distal part, female; *arrow* indicates distolateral setae of merus; (D and E) maxilla II, *arrow* indicates distomedial spiniform setae on endopod; (F and G) mandibular palp, lateral view; *arrow* indicates distolateral setae of article 2.

5′ Uropodal endopod without spiniform setae (Fig. 16.6.75 F); antennal scale length ∼2x antenna I peduncle length and 6x longer than wide (Fig. 16.6.69 E); telson cleft relatively shallow, obtusely angled, 0.1x length of telson; eyes nearly cylindrical, not produced beyond carapace lateral sides (Fig. 16.4.69 D); carapace width 2.5−2.7x eye length ..... *Mysis microphthalma* G. O. Sars, 1895 [Caspian Sea]

6(5) Carapace anterior width 3.1−3.3x eye length; eyes rather short, slightly narrowing distally, with small cornea (Fig. 16.6.77 E); antennal scale short, slightly longer than antenna I peduncle, ∼5x as long as wide; pereopod carpopropodi of eight articles; uropod endopod with 1−3 spiniform setae (Fig. 16.6.75 D) ..... *Mysis amblyops* G. O. Sars, 1907 [Caspian Sea]

6′ Carapace anterior width 2.3−2.5x eye length; eyes not narrowing distally, rather pyriform (Fig. 16.6.77 C); antennal scale long, >2x as long as antenna I peduncle, 6.7−6.9x as long as wide; pereopods carpopropodi of 12−14 articles; uropod endopod with 4−5 spiniform setae (Fig. 16.6.75 E) ..... *Mysis macrolepis* G. O. Sars, 1907 [Caspian Sea]

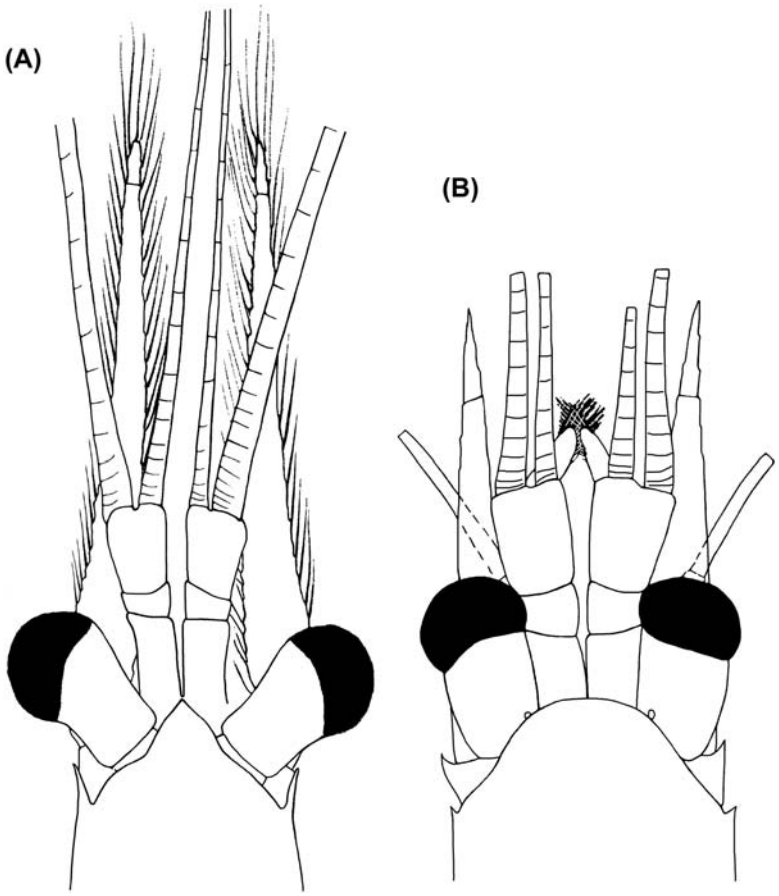


FIGURE 16.6.79 Heads of *Neomysis* species: (A) *N. integer*, female; (B) *N. japonica*, male (antennal scale setae not shown). *(B) From Ii (1964) with modifications.*

Mysida: Mysidae: *Diamysis*: Species

1 Pereopods: carpopropodus, dactylus and dactylar claw rather stout (Fig. 16.6.71 D); male pleopod IV exopod with a terminal strong seta only (Figs. 16.6.71 B) 2

1′ Pereopods: carpopropodus, dactylus, and dactylar claw rather slender (Fig. 16.6.71 E); male pleopod IV exopod with a terminal strong seta and a thin distal seta on article 1 (Fig. 16.6.72 C) ..... *Diamysis hebraica* Almeida Prado-Por, 1981 [Israel]

2(1) Eyes about twice as long as wide, with eye stalk produced beyond carapace lateral side (Fig. 16.6.76 A); telson 1.7−2x wider anteriorly than posteriorly, medial cleft armed with 20−36 spinulae (Fig. 16.6.76 C) ..... *Diamysis pengoi* Czerniavsky, 1882 [Sea of Azov, Black Sea, Marmara Sea basins]

2′ Eyes 1.3−1.4x as long as wide, with eye stalk not producing beyond carapace lateral side (Fig. 16.6.76 B); telson 2.7x wider anteriorly than posteriorly, medial cleft armed with about six spinulae (Fig. 16.6.76 D) ..... *Diamysis pusilla* G. O. Sars, 1907 [Caspian Sea]

Mysida: Mysidae: *Paramysis*: Species

1 Telson with lateral fine setules and spiniform setae (Fig. 16.6.81 A), telson cleft bearing usually 2−4 (rarely from 0 to 11) spinules (Figs. 16.6.82 C, D); maxilla II endopod article 2 with 1−3 distolateral spiniform setae (Figs. 16.6.81 E and 82 E) 2

1′ Telson with lateral spiniform setae only (Fig. 16.6.81 B−D), with or without small terminal cleft bearing 11−31 spinules; maxilla II endopod article 2 with setae only (Fig. 16.6.81 B) 6

2(1) Pereopod I carpopropodus article 4 subequal to article 3 (Fig. 16.6.82 B); maxilla II exopodal setae not visible in dorsal view (Fig. 16.6.82 D), maxilla II exopod narrowly ellipsoid (Fig. 16.6.82 E) 3

2′ Pereopod I carpopropodus article 4 is 60% length of article 3 (Fig. 16.6.82 A); maxilla II exopodal setae visible in dorsal view, protruding from carapace laterally near pleurocervical fissures (Fig. 16.6.82 C); maxilla II exopod widely ellipsoid or nearly rectangular (Figs. 16.6.82 F−H) 4

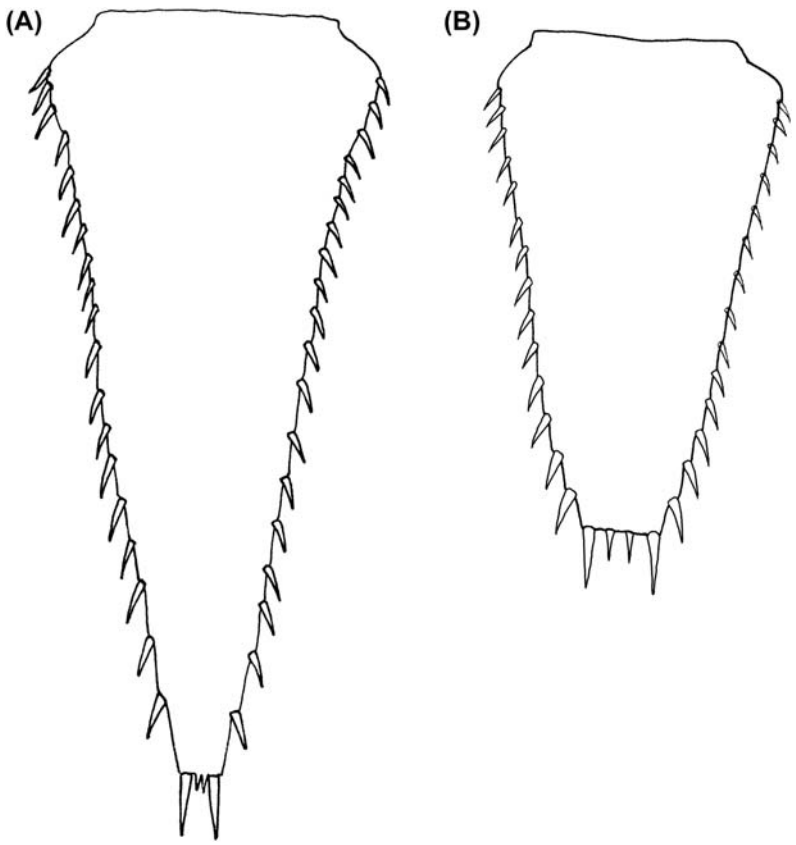


FIGURE 16.6.80 Telson of *Neomysis* species: (A) *N. integer*; (B) *N. awatschensis*.

3(2) Antennal scale distally truncated (distal margin not produced) (Fig. 16.6.84 A), ~2x length of antenna 1 peduncle or longer; telson longer than last abdominal segment, 3–4x as long as basal width ..... *Paramysis* (*Paramysis*) *kessleri kessleri* G. O. Sars, 1895 [Caspian Sea]

3′ Antennal scale distal margin produced (Fig. 16.6.84 B), scale shorter than 2x antenna I peduncle length; telson not longer than last abdominal segment, about 2x as long as basal width ..... *Paramysis* (*Paramysis*) *kessleri sarsi* Derzhavin, 1925 [Northwest Black Sea estuaries and rivers]

4(2) Antennal scale rather wide, length 2.5–3.0x width; telson cleft with two spinules (rarely up to 5) and with fine setae (Fig. 16.6.83 C); pereopod VI paradactylar setae smooth or finely serrated (Figs. 16.6.83 A, F); maxilla II exopod longer than wide (Figs. 16.6.82 G, H) 5

4′ Antennal scale length 3.1–3.5x width; telson cleft with 3–6 spinules (and sometimes up to 11), and without fine setae (Fig. 16.6.83 D); pereopod VI paradactylar setae strongly serrated (Fig. 16.6.83 B); maxilla II exopod wider than long (Fig. 16.6.82 F) .... *Paramysis* (*Paramysis*) *baeri* Czerniavsky, 1882 [Caspian Sea Basin]

5(4) Maxilla II exopod with long proximal and short distal setae (Fig. 16.6.82 G); telson lateral margins with 13–20 spiniform setae; pereopod ischia with rather sparse medial setation (Fig. 16.6.83 E) ..... *Paramysis* (*Paramysis*) *bakuensis* G. O. Sars, 1895 [Ponto-Caspian Basin]

5′ Maxilla II exopod with equally long proximal and distal setae (Fig. 16.6.82 H); telson lateral margins with 19–30 spiniform setae; pereopod ischia with rather dense medial setation (Fig. 16.6.83 F) ..... *Paramysis* (*Paramysis*) *eurylepis* G. O. Sars, 1907 [Caspian Sea]

6(1) Carapace anterior margin straight (Fig. 16.6.85 A); telson distal margin spinulae without lateral expansions (Fig. 16.6.85 B); pereopod merus rather short and broad, with curved setae (Fig. 16.6.85 D) 7

6′ Carapace anterior margin convex, smoothly rounded (Figs. 16.6.88 A, B); telson distal margin spinulae with lateral expansions (Fig. 16.6.85 C); pereopod merus rather narrow, with rather straight setae (Figs. 16.6.85 E and 88 F–H) 9

7(6) Antennal scale only slightly longer than antenna II peduncle, so that lateral spiniform seta base is approximately at level of antenna II peduncle anterior margin (Fig. 16.6.86 A); thoracopod exopod basal article without distal setae 8

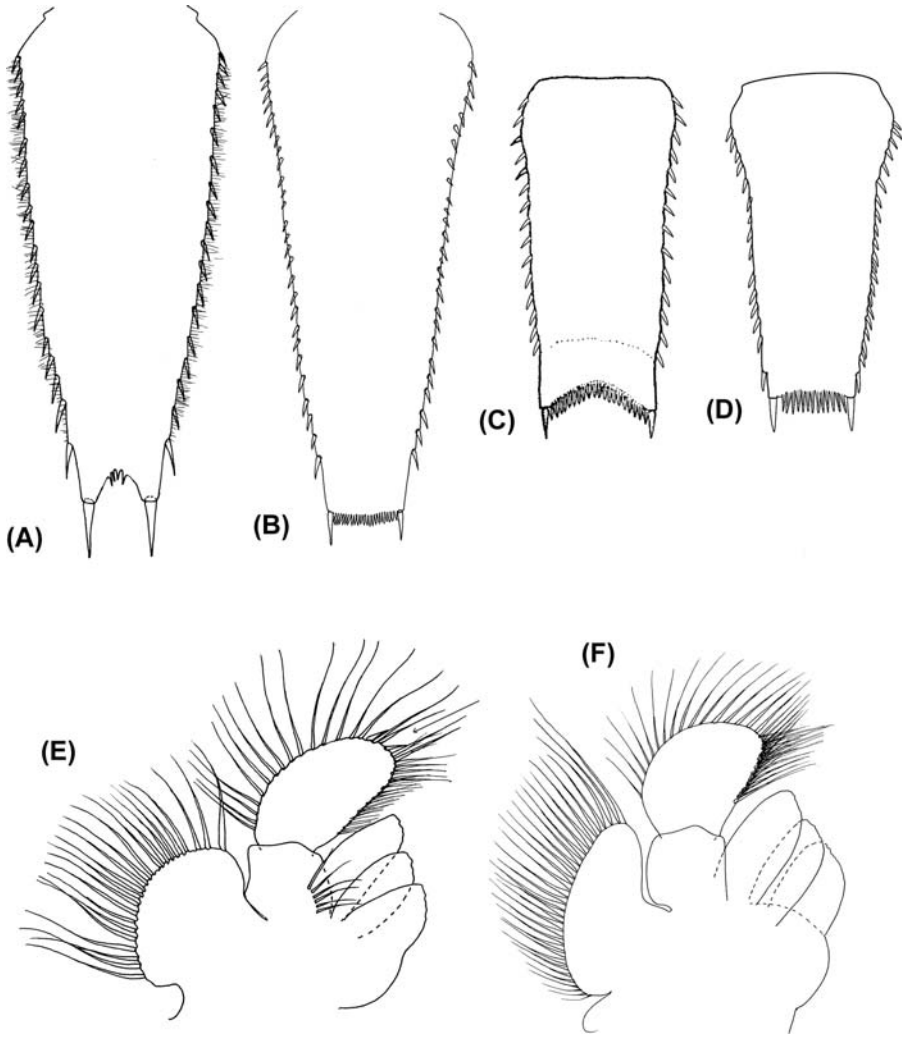


FIGURE 16.6.81 *Paramysis* species: (A) *P. (Paramysis) baeri*, telson; (B) *P. (Metamysis) grimmi*, telson; (C) *P. (Serrapalpisis) lacustris*, telson; (D) *P. (Mesomysis) intermedia*, telson; (E) *P. (Paramysis) eurylepis*, maxilla II (setae of endites not shown); *arrow* indicated distolateral spiniform setae; (F) *P. (Metamysis) inflata*, maxilla II (setae of endites not shown).

7′ Antennal scale considerably longer than antenna II peduncle, so that lateral spiniform seta base extends far beyond antenna II peduncle anterior margin (Fig. 16.6.86 B); thoracopod exopod basal article with distal setae (Fig. 16.6.85 F) ..... *Paramysis* (*Metamysis*) *grimmi* G. O. Sars, 1895 [Caspian Sea]

8(7) Carapace anterior part narrower than first abdominal segment; antennal scale narrow, 3.5−4x longer than wide (Fig. 16.6.69 J); pereopod I ischium 4.0−4.5x as long as wide ..... *Paramysis* (*Metamysis*) *ullskyi* Czerniavsky, 1882 [Ponto-Caspian Basin. Invasive in west Palearctic]

8′ Carapace anterior part as wide as first abdominal segment; antennal scale rather wide, 2.5−2.7x as long as wide; pereopod I ischium 3.0−3.5x as long as wide ..... *Paramysis* (*Metamysis*) *inflata* G.O. Sars, 1907 [Caspian Sea]

9(6) Telson subequal or longer than last abdominal segment; antennal scale lanceolate (lateral spiniform seta in distal half of margin) (Fig. 16.6.87 A) 10

9′ Telson shorter than last abdominal segment; antennal scale rhombic (lateral spiniform seta approximately in the middle of margin) (Fig. 16.6.87 B) ..... *Paramysis* (*Nanoparamysis*) *loxolepis* G. O. Sars, 1895 [Caspian Sea]

10(9) Telson cleft (Fig. 16.6.81 C), cleft with 19−30 spinules; mandibular palp article 2 with posterior setae robust, serrated (Figs. 16.6.88 C−E) 11

10′ Telson uncleft (Fig. 16.6.81 D), apical margin with 11−17 spinulae; mandibular palp article 2 with posterior setae thin, smooth ..... *Paramysis* (*Mesomysis*) *intermedia* Czerniavsky, 1882 [Ponto-Caspian Basin. Invasive in Eastern Europe]

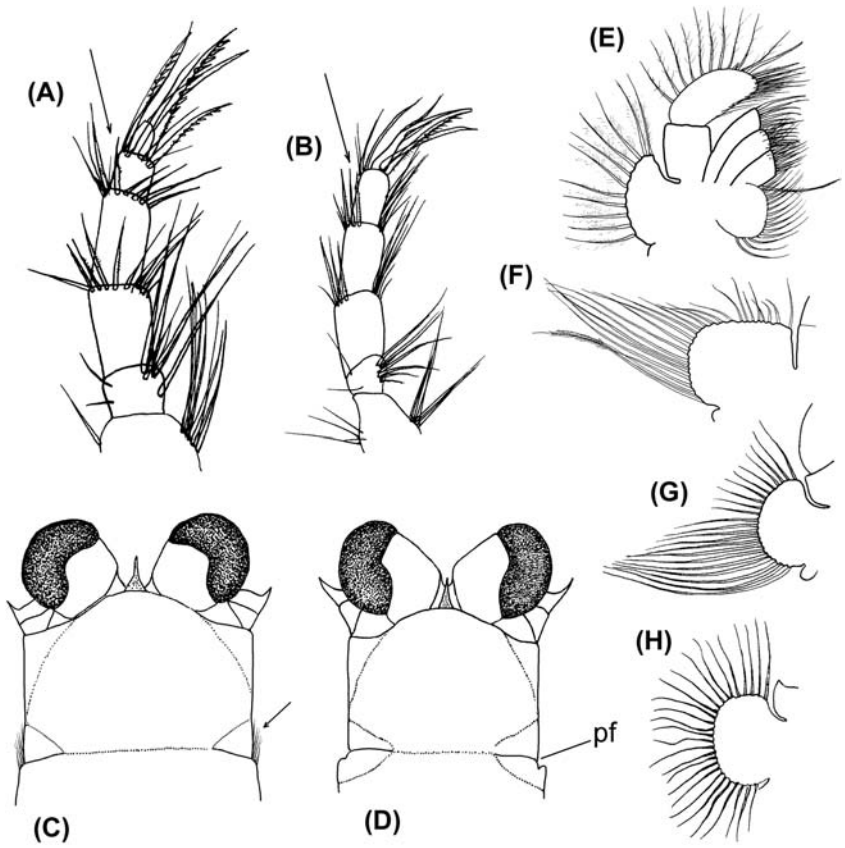


FIGURE 16.6.82 *Paramysis (Paramysis)* species: Carpopropodus; *arrow* indicates article 4; (A) *P. baeri*; (B) *P. kessleri kessleri*. Head (appendages not shown) (C) *P. eurylepis*, *arrow* indicates setae of maxilla II exopod, projecting near pleurocervical fissures (pf). (D) *P. kessleri kessleri*. Maxilla II (exopod): (E) *P. kessleri sarsi*; (F) *P. baeri*; (G) *P. bakuensis*; (H) *P. eurylepis*.

11(10) Antennal scale subequal to antenna I peduncle (Fig. 16.6.88 A); pereopod merus with 4–8 medial setal clusters (Figs. 16.6.88 F, G) 12

11′ Antennal scale length ~1.5x antenna I peduncle length (Fig. 16.6.88 B); pereopod merus with 14–17 medial setal clusters (Fig. 16.6.88 H) ..... *Paramysis* (*Serrapalpisis*) *incerta* G. O. Sars, 1895
[Caspian Sea]

12(11) Mandibular palp article 2 with fine medial setae, bearing barely visible serrations (Figs. 16.6.88 C, D); pereopod merus with 4 or 5 (rarely 6) medial setal clusters (Fig. 16.6.88 G); carpopropodus articles medial margins without medial setae (Fig. 16.6.88 G) 13

12′ Mandibular palp article 2 with fine medial setae, bearing rough serrations (Fig. 16.6.88 E); pereopod merus with 6–8 medial setal clusters (Fig. 16.6.88 F); carpopropodus articles medial margins with medial setae (Fig. 16.6.88 F) ..... *Paramysis* (*Serrapalpisis*) *sowinskii* Daneliya, 2002
[Sea of Azov Basin, Caspian Sea]

13(12) Carapace not inflated anteriodorsally in lateral view (Fig. 16.6.89 A); paradactylar falciform setae with spinulae along entire margin (Figs. 16.6.89 C, D) ..... *Paramysis* (*Serrapalpisis*) *lacustris* (Czerniavsky, 1882)
[Ponto-Caspian Basin. Invasive in Eastern Europe]

13′ Carapace anteriodorsally inflated in lateral view (Fig. 16.6.89 B); paradactylar falciform setae with spinulae only in proximal half (Fig. 16.6.89 E) ..... *Paramysis* (*Serrapalpisis*) *kosswigi* Băcescu, 1948
[Turkey]

Stygiomysida: Species

1 Penultimate thoracic segment with dorsal scale (Fig. 16.6.67 A); uropodal protopod with short ventral medial lobe, bearing long apical and short medial spiniform setae (Fig. 16.6.67 C); uropodal exopod of two articles (Fig. 16.6.67 C) ..... Lepidomysidae, one species: *Spelaeomysis bottazii* Caroli, 1924
[Hypogean, Southern Italy]

1′ Penultimate thoracic segment with no dorsal scale; uropodal protopod with long ventral medial process, bearing about seven distal and medial spiniform setae and numerous short spinules (Fig. 16.6.67 D); uropodal exopod uniarticulate (Fig. 16.6.67 D) ..... Stygiomysidae, one species: *Stygiomysis hydruntina* Caroli, 1937
[Hypogean, Southern Italy]

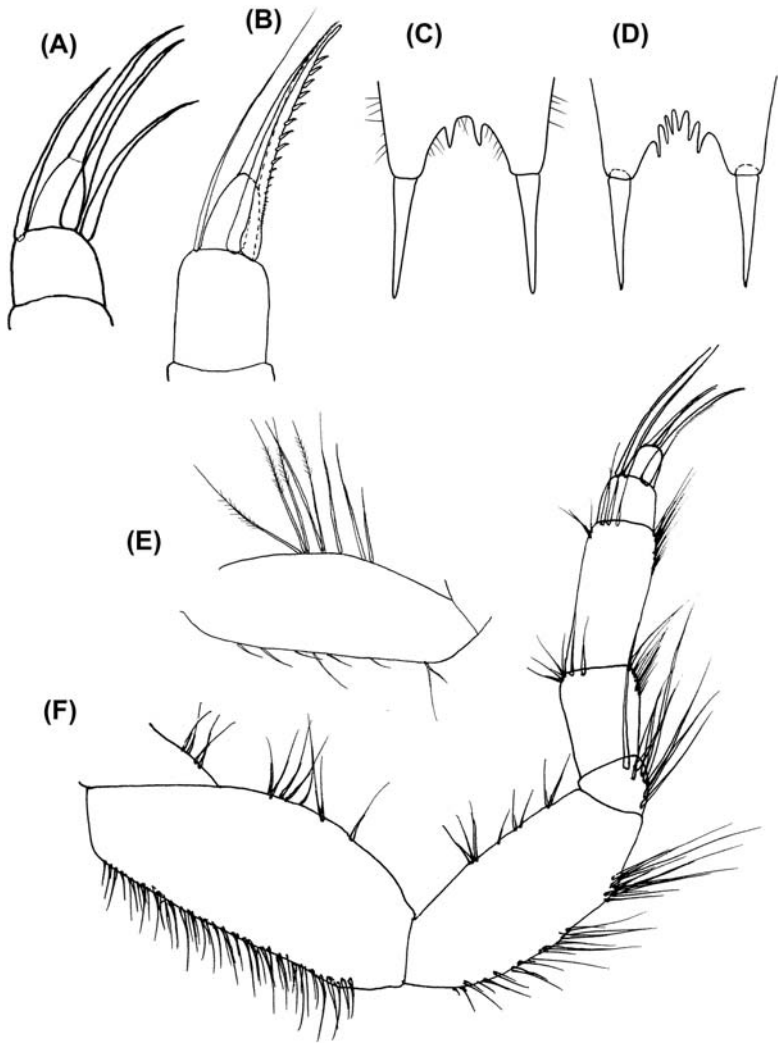


FIGURE 16.6.83 *Paramysis (Paramysis)* species: Pereopod V paradactylar setae for: (A) *P. bakuensis*, (B) *P. baeri*. Telson cleft for: (C) *P. bakuensis*; (D) *P. baeri*. Pereopod VI ischium, male (E) *P. baeri*. Pereopod V1 endopod, male: (F) *P. eurylepis*.

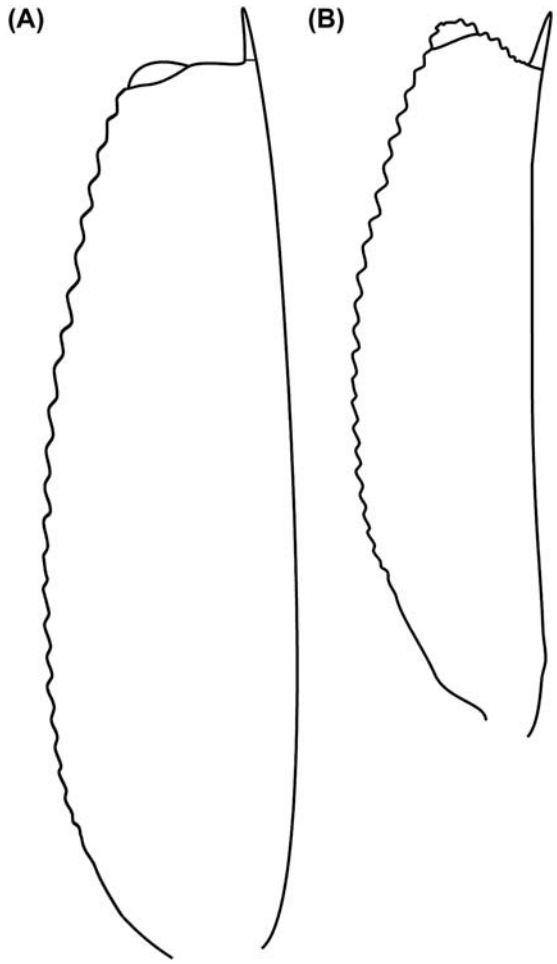


FIGURE 16.6.84 *Paramysis (Paramysis) kessleri* subspecies: Antennal scale (setae not shown) for: (A) *P. kessleri kessleri*; (B) *P. kessleri sarsi*.

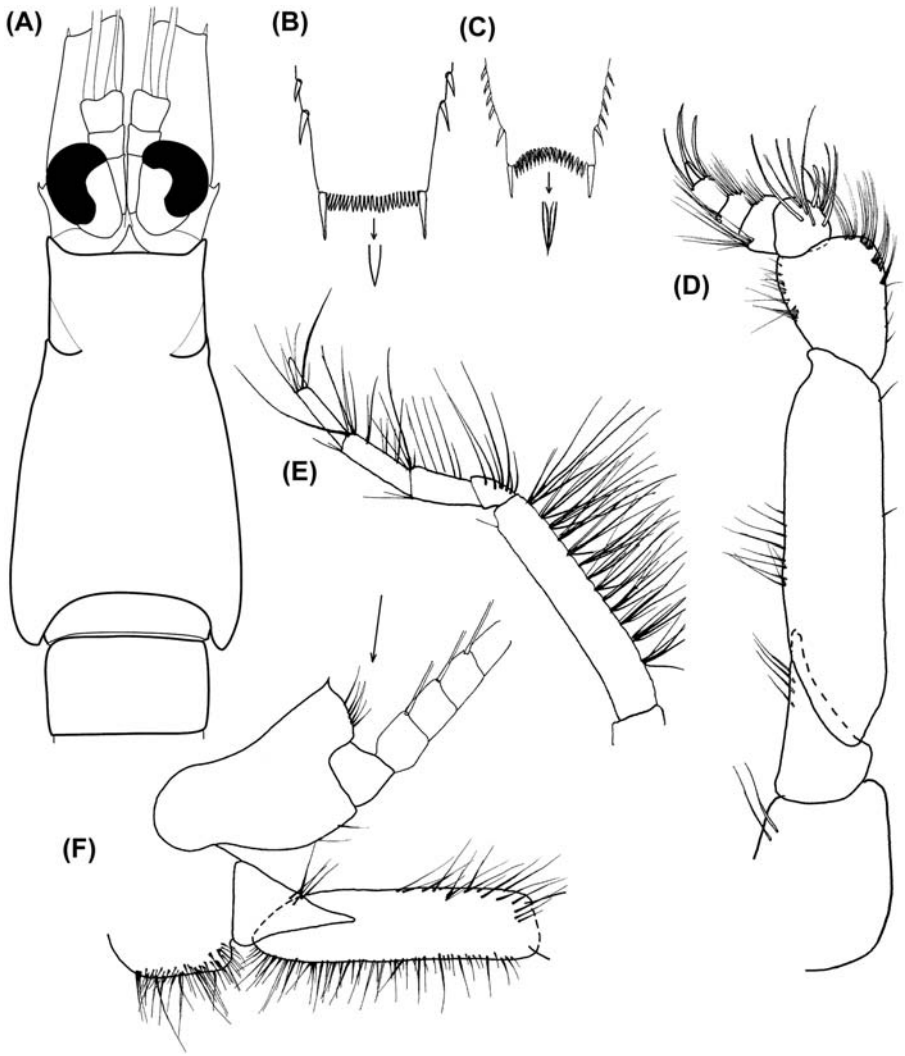


FIGURE 16.6.85 *Paramysis* species: (A) *P. (Metamysis) grimmi*, cephalothorax, female; (B) *P. (Metamysis) grimmi*, posterior part of telson and enlarged spinule; (C) *P. (Nanoparamysis) loxolepis*, posterior part of telson and enlarged cleft spinule; (D) *P. (Metamysis) grimmi*, pereopod VI endopod; (E) *P. (Nanoparamysis) loxolepis*, pereopod VI endopod distal part (merus, carpopropodus, and dactylus); (F) *P. (Metamysis) grimmi*, pereopod I proximal part; *arrow* indicates setae of exopod basal article.

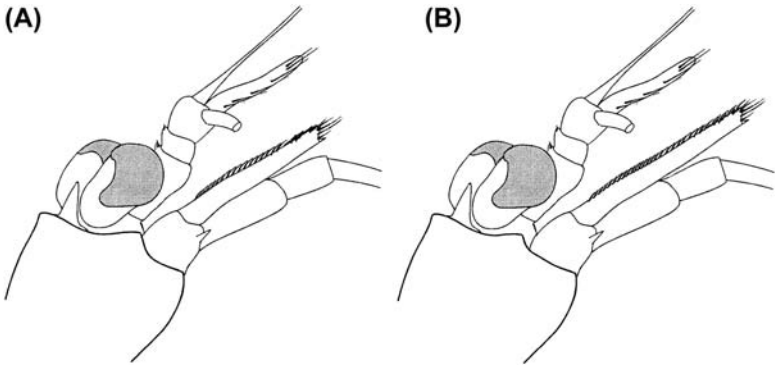


FIGURE 16.6.86 *Paramysis (Metamysis)* species: head, lateral view, male: (A) *P. inflata*; (B) *P. grimmi*.

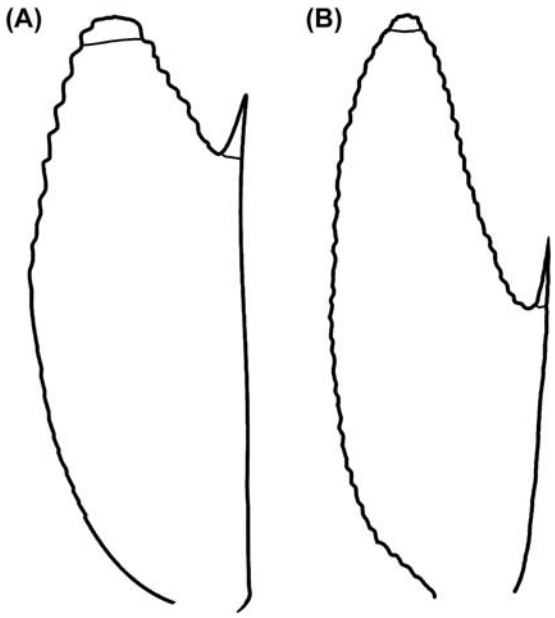


FIGURE 16.6.87 *Paramysis* species: antennal scale: (A) *P. (Mesomysis) intermedia*; (B) *P. (Nanoparamysis) loxolepis*.

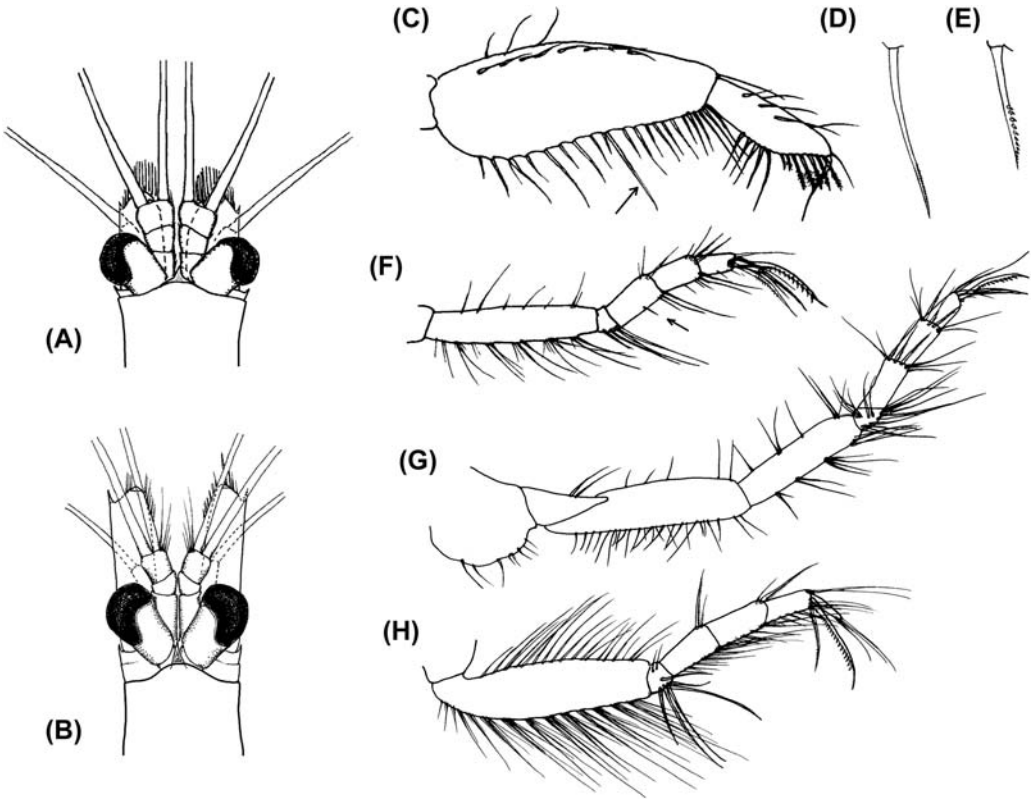


FIGURE 16.6.88 *Paramysis (Serrapalpisis)* species: head, female (A) *P. lacustris*; (B) *P. incerta*; mandibular palp; *arrow* indicates medial setae of article 2: (C) *P. lacustris*; (D) *P. lacustris*, medial seta; (E) *P. sowinskii*, medial seta; (F) *P. sowinskii*, distal part of pereopod I endopod; *arrow* indicates median setae of carpopropodus articles; (G) *P. lacustris*, pereopod I endopod; (H) *P. incerta*, distal part of pereopod VI endopod.

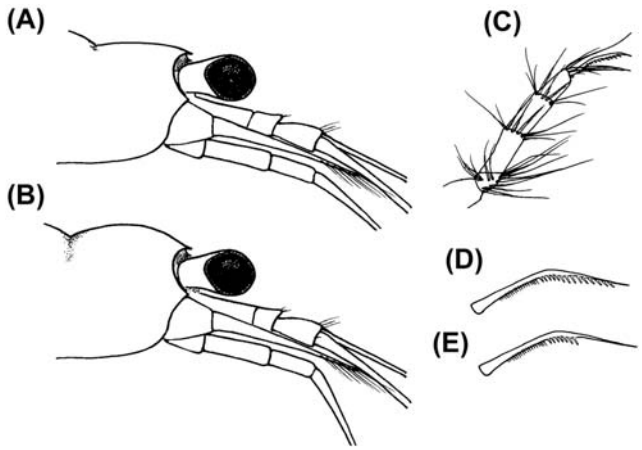


FIGURE 16.6.89 *Paramysis (Serrapalpisis)* species: head, lateral view, female: (A) *P. lacustris*, (B) *P. kosswigi*. (C) *P. lacustris*, carpopropodus and dactylus with paradactylar falciform setae; Paradactylar falciform seta: (D) *P. lacustris*, (E) *P. kosswigi*.

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